

FERNS AND FERN ALLIES OF GUATEMALA

This is the second of a three-part series dealing with the fern flora of Guatemala. "Part I: Ophioglossaceae through Cyatheaceae," was printed in *Fieldiana, Botany*, Volume 39, 1976. The present part contains the treatment of 67 genera under the huge and highly diverse family Polypodiaceae (*sens. lat.*). A third and final part will include the water ferns Marsileaceae and Salviniaceae, the "fern allies," and an index to the entire fern flora.

In the present publication, a key to the 67 genera of Polypodiaceae is provided, and descriptions and discussions of each genus follow, in alphabetical order. Each of the generic treatments contains a key to the species and at least one drawing illustrating the characteristic features of the genus. Each of these descriptions contains some reference to the various features of the spores, and in most cases the latter are described as "with" or "without" perine. The statement may be misleading, for enough work has been done recently to indicate that most (if not all) fern spores *are* provided with perine (perispore), although often such may not be evident without the aid of a transmission electron microscope. (For further information see: Lugardon, *Pollen et Spores* 14: 227-261. 1972; and 16: 161-226. 1974; Kramer, *Gard. Bull.* 30: 79-83. 1977.) Let it be understood, therefore, that when perine is described as "lacking," it is meant that such is not evident at least through usual optical aids.

Work on the genus *Elaphoglossum* has been done by John T. Mickel (New York Botanical Garden) and that on *Thelypteris* by Alan R. Smith (University of California, Berkeley). To both of these, my good friends, I owe a deep debt of gratitude. The two genera are among the largest and most difficult of all the ferns, and yet each of these men has presented a superb treatment which clearly and fully defines the Guatemalan species and their relationships. I would also like to thank Alan Smith for his help on other genera treated herein. Our exchange of ideas on taxonomic problems, personally and in correspondence, has been of great benefit to me.

As in Part I of the "Ferns and Fern Allies of Guatemala," research has been based chiefly on the excellent fern collection at Field Museum of Natural History. Additionally, over 3,000 specimens have been borrowed from the following institutions: U.S. National Herbarium, Washington, D.C.; University of California, Berkeley; Gray Herbarium, Cambridge, Massachusetts; New York Botanical Garden, Bronx, New York; Museo de Historia Natural, Guatemala City, Guatemala; Royal Botanical Gardens, Kew, England; Muséum National d'Histoire Naturelle, Paris, France. I would like to express my gratitude to the curators of these herbaria for sending their specimens for study.

I especially wish to thank Dr. David Lellinger, U.S. National Herbarium, not only for the many courtesies extended to me on my frequent visits, but also for the stimulating and enlightening discussions on taxonomic problems of the numerous species common to both our areas of research.

The illustrations are the result of the collaboration between five different artists: Zorica G. Dabich, Yale Factor, Marion Pahl, William Peterson, and Richard Roesener. Their careful study, painstaking efforts, and patience have produced the superb drawings which clarify so many details of the verbal descriptions. I am indebted to all of them.

Dr. Louis O. Williams, former Chairman of Botany at Field Museum and chief collaborator (with Paul C. Standley) on the recently completed "Flora of Guatemala," retired from work at the Museum some time ago. It was at his insistence that I began this fern flora, and his steady hand and wise counsel have been a constant source of help and encouragement to me. My deepest expressions of appreciation can scarcely appear adequate.

All abbreviations of periodical publications follow the system of *Botanico-Periodicum-Huntianum*, Hunt Botanical Library, Pittsburgh, Pennsylvania, 1978.

POLYPODIACEAE

REFERENCES: W. R. Maxon, Polypodiaceae, in: *Pteridophyta of Porto Rico and the Virgin Islands*, Sci. Surv. 6: 391-494. 1926. R. C. Ching, On the natural classification of the family Polypodiaceae, *Sunyatsenia* 5: 201-268. 1940. A. H. G. Alston, The subdivision of the Polypodiaceae, *Taxon* 5: 23-25. 1956. E. R. de la Sota, Polypodiaceae y

Grammitidaceae Argentinas, Opera Lilloana 5: 1-229. 1960. R. M. Tryon, The ferns of Peru—Polypodiaceae (Dennstaedtieae to Olean-dreae), Contr. Gray Herb. 194: 1-253. 1964.

Plants terrestrial, epiphytic, or epipetric (or aquatic in *Ceratopteris*), greatly diverse in size and shape; rhizome long- or short-creeping to ascending or erect, provided with scales or trichomes, or occasionally glabrous; leaves widely spaced to fasciculate, monomorphic or dimorphous, simple and entire to 4-pinnate or more, circinate in veneration; veins free to areolate, the areoles with or without free, included veinlets; sporangia grouped in definite sori or coenosori, or loosely clustered in lines or bands, or without definite pattern; individual sporangia thin-walled (1 cell thick), long-stalked (or rarely the stalk short to vestigial), with a vertical annulus which encircles the capsule but is interrupted by the stalk (or annulus vestigial or nearly so in *Ceratopteris*); indusium present or lacking, often formed by the modified segment margin; spores mono-lete and bilateral to trilete and tetrahedral or subglobose, white to brown or blackish, or, in a few genera, ripe ones green (containing chlorophyll).

The family is a huge and unwieldy one, with its genera so diverse as to nearly defy circumscription. It contains perhaps two-thirds of the ferns now living, the total being estimated by various authors at 150-180 genera and 6,000-10,000 species. Great, often heated, controversy has raged since the dawn of Taxonomy, as to whether the species ought to be grouped in a single family or segregated into 10-30 smaller families (or subfamilies). Yet after all this time there has emerged no majority of opinion offering an adequate solution. It would certainly be more desirable and convenient to be able to recognize and communicate 10 or more smaller families, but none of the attempts thus far has succeeded to an appreciable degree. An outstanding example can be made of Copeland's circumscription of the "Families" in his *Genera Filicum* (1947) where, in the key, Polypodiaceae (*sens. strict.*) appears 9 times, and the segregates "Aspidiaceae" and "Pteridaceae" 11 times each! This obviously affords no more convenient or practical an approach than the recognition of one huge family. Thus, for purposes of this treatment, the more conservative approach is adopted, in which 67 genera of Guatemalan ferns are grouped within the Polypodiaceae.

N.B. A key to the genera of Polypodiaceae follows, and a word of caution is tendered to the reader. The characters are often, *but not always*, those of the genus in its broadest sense; *i.e.*, it has sometimes been desirable to use principal features of the genus as they occur in the species represented in Guatemala. (For example, a genus may contain both areolate- and free-veined species, but only species with free veins occur in Guatemala. Therefore the genus will be keyed out under free-veined species.) On the other hand, the reader will find *all* features of the genus listed within each generic description, with

notes, when applicable, on how the Guatemalan species may vary within this context.

KEY TO THE GENERA OF POLYPODIACEAE IN GUATEMALA

- a. Plants aquatic or semiaquatic, floating on or rooted beneath the water.
Ceratopteris.
- a. Plants neither aquatic nor semiaquatic.
 - b. Sporangia confined to, or borne very near, the lamina or segment margin (or segment tip), not extending far from it, never spreading to or near the costa.
 - c. Leaves simple, essentially entire.
 - d. Sporangia immersed in shallow or deep, continuous, submarginal grooves; areoles lacking included, free veinlets.
 - e. Areoles in a single series between costa and leaf margin. *Vittaria*.
 - e. Areoles in 3-5 series between costa and leaf margin. *Ananthacorus*.
 - d. Sporangia superficial, borne in continuous or interrupted, marginal or sub-marginal lines; areoles with included, free veinlets.
 - f. Sori provided with marginal indusia; leaves subdimorphous, the fertile lamina much narrower than the sterile. *Dictyoxiphium*.
 - f. Sori exindusiate; leaves essentially monomorphous (although tips of fertile ones often somewhat constricted). *Paltonium*.
 - c. Leaves pinnatifid to decompound (rarely only deeply lobed).
 - g. Rhizome pubescent, lacking scales.
 - h. Sorus somewhat to greatly elongated and subcontinuous along segment margin, served by 2 to many vein branches.
 - i. Leaf tissue thin- to firm-herbaceous; veins few and widely spaced in each ultimate segment, commonly 3-6 mm. apart; sori relatively short, borne at or near the sinuses between segments and usually served by 2-4 veins or branches. *Lonchitis*.
 - i. Leaf tissue chartaceous to subcoriaceous; veins numerous and crowded in each segment, rarely more than 1 mm. apart; sori long, often extending from sinus to (or around) tips of segments, and served by numerous veins. *Pteridium*.
 - h. Sorus short, borne at the tip of a single vein or branch.
 - j. Indusium purse- or cup-shaped (somewhat bivalvate), with a true, inner indusium joined to an opposed, outer half formed by a modified lobe of leaf tissue. *Dennstaedtia*.
 - j. Indusium (or pseudindusium) consisting of a slightly to strongly modified lobe of the leaf segment, the lobe not or strongly reflexed. . *Hypolepis*.
 - g. Rhizome scaly (the scales sometimes filamentous or mixed with simple trichomes).
 - k. Veins copiously areolate, the areoles commonly enclosing secondary areoles and free veinlets which spread in all directions. X *Pleuroderris*.
 - k. Veins free or, if areolate in some species, the areoles not with free, included veinlets.
 - l. Indusium attached at its sides and/or base, opening outward or in all directions.
 - m. Pinnae simple, articulate to the rachis; indusium circular to reniform or lunate, attached at a point or sinus. *Nephrolepis*.
 - m. Pinnae simple to 4-pinnate, not articulate; indusium narrow, flaplike,

- continuous or subcontinuous and attached along a rather broad base, or cup- or purse-shaped and attached along its sides and/or base.
- n. Leaves indeterminate, lamina 3- to 4-pinnate, the ultimate segments or lobes linear to cuneiform, 0.2-1 mm. broad; sori borne singly at the very tip of a segment, indusium distinctly bilabiate. . . *Odontosoria*.
 - n. Leaves determinate; lamina 1- to 4-pinnate, the ultimate segments or lobes 3 mm. broad or (commonly) very much broader; sori several to numerous along the segment or pinna margin; indusium not or obscurely bilabiate (if one sorus to a segment the indusium linear and subcontinuous along the margin).
 - o. Ultimate segments dimidiate. *Lindsaea*.
 - o. Ultimate segments not or scarcely dimidiate (sometimes somewhat inequilateral at the base). *Saccoloma*.
 - l. Indusium (or pseudindusium) attached at pinna or segment margin or formed by the reflexed margin, opening inward, or lacking.
 - p. Sori borne on the undersurface of the modified, reflexed segment lobe or flap which serves as an indusium; ultimate segments typically flabellate or dimidiate; veins dichotomously branched. *Adiantum*.
 - p. Sori exindusiate, or if protected by an indusium, not borne on its undersurface; ultimate segments neither flabellate nor dimidiate; veins pinnately arranged.
 - q. Fertile vein tips connected by a continuous or subcontinuous marginal commissure, on which is borne the sorus; veins otherwise free or areolate.
 - r. Petiole and rachis lustrous, atropurpureous to blackish, commonly much longer than the lamina; lamina pedate or subpedate, 6-12 cm. long. *Doryopteris*.
 - r. Petiole and rachis stramineous to dark brown, shorter than the lamina; lamina 1- to 4-pinnate, large to huge (commonly well over 20 cm.).
 - s. Pinnae sessile, the basal pinnules strongly overlapping the rachis (often reduced and stipule-like); rhizome scales clathrate, sometimes reduced to or intermixed with septate trichomes; veins areolate, at least along the costa. *Histiopteris*.
 - s. Pinnae stalked, or if sessile, the basal pinnules not stipule-like or strongly overlapping the rachis; rhizome scales not or scarcely clathrate, not intermixed with trichomes; veins free, or in some species partially or wholly areolate. *Pteris*.
 - q. Fertile vein tips free, not connected by a marginal commissure; veins otherwise free.
 - t. Sorus indusiate, the indusium inframarginal (sometimes inconspicuously so) and much thinner (often scarious) than the segment margin; rachis abaxially glabrous, adaxially densely covered with minute, stout, cylindrical to subclavate, 1- to 2-celled trichomes. . . *Mildella*.
 - t. Sorus exindusiate, or protected by the reflexed segment margin which may or may not be strongly modified into a distinct indusium; rachis glabrous or variously pubescent or scaly, but not densely covered adaxially with cylindrical to subclavate 1- to 2-celled trichomes.

- u. Lamina with margins of fertile segments strongly reflexed or revolute and often strongly modified, the surface not farinose, or rarely so (in 2 species of *Cheilanthes*) and then the margins conspicuously modified into thin, scarious indusia.
- v. Indusia continuous, consisting of the strongly revolute, scarcely modified segment margin (young plants of *P. skinneri* may have greatly modified indusia); ultimate segments not farinose, not (or rarely) pubescent or scaly, never bead-like. *Pellaea*.
- v. Indusia continuous or interrupted, consisting of the strongly revolute or reflexed segment margin which is commonly greatly modified (lighter in color and thinner in texture); ultimate segments glabrous to pubescent, scaly or farinose, in many species beadlike. *Cheilanthes*.
- u. Lamina with margins of fertile segments not or scarcely reflexed, or rarely so (in 2 species of *Notholaena*) and then the margins not strongly modified, the abaxial surface farinose or not.
- w. Lamina pentagonal, densely pilose abaxially, not farinose. ... *Bommeria*.
- w. Lamina not pentagonal, or if so the abaxial surface densely white- or yellow-farinose. *Notholaena*.
- b. Sporangia not exclusively marginal or submarginal, although in some genera spreading in lines or masses across most or all of the area between costa and margin.
- x. Sporangia protected by true indusia, these roundish, or elongated to linear, sometimes inconspicuous and/or fugacious (or in some species of *Blechnum* sporangia forming a continuous mass between costa and point of attachment of the linear indusium).
- y. Indusium globose, cyathiform, cucullate, oblong or linear, fully or partly enveloping the sorus, or linearly attached (in *Athyrium* sometimes inequilaterally reniform).
- z. Veins areolate.
 - aa. Leaves simple, entire, to 8 cm. long; veins flabellate. ... *Schaffneria*.
 - aa. Leaves pinnate or pinnate-pinnatifid, 0.5-2 m. long; veins not flabellate.
 - bb. Lamina simply pinnate, firm-herbaceous; sori linear, in parallel lines, spreading obliquely, well away from the costa; indusium thin, essentially plane. *Hemidictyum*.
 - bb. Lamina pinnate-pinnatifid, chartaceous to subcoriaceous; sori oblong, a single one borne in, and nearly filling the costular areole; indusium thick, convex. *Woodwardia*.
- z. Veins essentially free (fertile ones in *Blechnum* connected by a commissure).
 - cc. Sorus borne on a commissure connecting the veins and which runs parallel to the costa. *Blechnum*.
 - cc. Sorus borne on or along the veins, the latter not connected by a commissure.
 - dd. Indusium attached at a point on its base, either hemispherical to ovate-lanceolate or globose to cyathiform.
 - ee. Indusium hemispherical, ovate or ovate-lanceolate, arching over the sporangia; rhizome scales concolorous. *Cystopteris*.

- ee. Indusium globose, partially breaking away at maturity and becoming irregularly cyathiform; rhizome scales commonly bicolorous. . . .
Woodisia.
- dd. Indusium linearly attached along a vein, either medially or at one edge, opening on both sides or only on one side, commonly linear to elliptic or oblong.
- ff. Indusium attached along a medial line, opening on both sides; costae and costules adaxially provided with short awns; ultimate segments somewhat articulate to the costa. *Didymochlaena.*
- ff. Indusium attached by one edge to (and opening on) the acroscopic side of a vein, or others attached to (and opening on) the basiscopic side; costae and costules lacking awns; ultimate segments not articulate.
- gg. Rhizome scales clathrate, the lumina commonly clear and often transparent; sori confined to the acroscopic side of veins (or in a few species some sori paired back-to-back). *Asplenium.*
- gg. Rhizome scales not or obscurely clathrate, the cell walls brownish; sori (at least some of them) paired back-to-back, or else borne on the acroscopic side of veins and distally hooking over to the basiscopic side.
- hh. Sori single and (some of them) double, borne on either one side of a vein or the other. *Diplazium.*
- hh. Sori single, never double, borne on the acroscopic side of a vein, but distally hooking over it and partially doubling back on the basiscopic side. *Athyrium.*
- y. Indusium reniform to circular-peltate, attached to the vein at a sinus or point.
- ii. Leaves or pinnae articulate.
- jj. Leaves simple; petiole conspicuously articulate near or above the base.
Oleandra.
- jj. Leaves pinnate; petiole not articulate, but pinnae articulate to the rachis.
- kk. Sori in 1-3 (commonly 2) rows between costa and pinna margin, at least 1 row very near the costa. *Cyclopeltis.*
- kk. Sori in a single row, supramedial or submarginal, between costa and each margin. *Nephrolepis.*
- ii. Leaves or pinnae not articulate.
- ll. Leaves conspicuously dimorphous, fertile segments strongly constricted, often so much so that sori are as broad as the segment. . . . *Maxonia.*
- ll. Leaves not or scarcely dimorphous.
- mm. Ultimate segments, or pinna margins (especially at the apex), spinulose or spinulose-serrate.
- nn. Lamina simply pinnate, terminating in a conform, apical segment. *Cyrtomium.*
- nn. Lamina 2- to 5-pinnate, rarely 1-pinnate and if so gradually reduced to a nonconform, pinnatifid apex.
- oo. Lamina pinnate to 2-pinnate, or rarely 2-pinnate-pinnatisect. . .
Polystichum.
- oo. Lamina 3- to 5-pinnate. *Arachniodes.*
- mm. Ultimate segments entire to variously dentate or serrate, but without conspicuous, cartilaginous spines.
- pp. Veins copiously areolate, the areoles with free, included veinlets

- which spread in various directions (or if free veinlets are rare or lacking, then the lamina 2-pinnate-pinnatifid or more). . *Tectaria*.
- pp. Veins free, or if connivent or merging and with free, included veinlets, then the free veinlets excurrent and the lamina pinnate or pinnate-pinnatifid.
- qq. Axes sulcate adaxially, the groove flanked by distinct ridges which are conspicuous and continuous as ridges (or as thickened leaf margins) on the axis of the next order above or below.
- rr. Rachis and costae (especially adaxially) rather copiously puberulent, the trichomes pluricellular, septate, and reddish brown. *Lastreopsis*.
- rr. Rachis and costae glabrous or scaly, or with unicellular, cylindrical, hairlike glands (sometimes the scales narrow and hairlike), but lacking septate, pluricellular trichomes. *Dryopteris*.
- qq. Axes not sulcate, or if so the ridges not or obscurely continuous as ridges on the axes of the next order above or below.
- ss. Indusium peltate; leaves less than 10 cm. long, copiously glandular throughout (on rhizome scales, axes, lamina surfaces, and indusia). *Adenoderris*.
- ss. Indusium reniform, leaves commonly much longer than 10 cm. (often huge), sometimes with various types of glands, but not consistently glandular on all leaf parts.
- tt. Trichomes of petiole, rachis, and often costae unbranched, pluricellular, septate, short, stout, and reddish brown (these sometimes intermixed with scales and/or longer, paler trichomes). *Ctenitis*.
- tt. Trichomes of major axes branched or unbranched, unicellular, or if pluricellular then long, thin, and pale. . . *Thelypteris*.
- x. Sporangia exindusiate (sometimes partly protected by a reflexed segment margin or, in *Onocleopsis*, a vestigial, scalelike indusium rarely present), in discrete sori, or spreading in masses or lines or indefinite clusters across part or all of the abaxial surface.
- uu. Sporangia in dense masses, obscuring all or most of the fertile lamina or segment, leaf margins not reflexed nor the surface farinose.
- vv. Sterile lamina simple and entire. *Elaphoglossum*.
- vv. Sterile lamina pinnate to 3-pinnate, or flabellate and dichotomously dissected.
- ww. Leaves rarely over 10 cm. long; sterile lamina flabellate and dichotomously dissected. *Peltapteris*.
- ww. Leaves 0.3-3 m. long; sterile lamina pinnate to 3-pinnate.
- xx. Leaves not or scarcely dimorphous, caespitose (not climbing); paraphyses conspicuous in the sori. *Acrostichum*.
- xx. Leaves dimorphous or subdimorphous; rhizome creeping to scandent (often high-climbing) with leaves somewhat to widely spaced; paraphyses lacking.
- yy. Veins copiously areolate, the areoles with free, included veinlets, these excurrent or (typically) spreading in various directions. . . *Bolbitis*.

- yy. Veins free, rarely merging, or joined at their apices by a submarginal strand, but in any case lacking free, included veinlets.
- zz. Pinnæ articulate to the rachis, sterile and fertile ones simple. . .
Lomariopsis.
- zz. Pinnæ not articulate, sterile ones simple to 2-pinnate, fertile ones pinnate or more. *Polybotrya*.
- uu. Sporangia arranged in definite sori or coenosori, or spreading in lines or indefinite patterns across the leaf surface, occasionally confluent at maturity, sometimes partly protected by a farinose coating or by a reflexed segment margin.
- aaa. Leaves conspicuously dimorphous, the fertile lamina 2- to 3-pinnate.
- bbb. Leaves partly dimorphous, the fertile ones soriferous only in the distal half; sterile lamina 2-pinnate to (usually) 3-pinnate, with veins free. . .
Llavea.
- bbb. Leaves fully dimorphous, the fertile ones wholly soriferous; sterile lamina pinnate or (sometimes) pinnate-pinnatisect, with veins copiously anastomosing. *Onocleopsis*.
- aaa. Leaves essentially monomorphous, or if dimorphous the fertile lamina merely simple or pinnatifid.
- ccc. Leaves simple and entire; sporangia grouped in greatly elongated to linear sori or coenosori or following the veins in indefinite patterns; lamina glabrous.
- ddd. Sporangia joined in a long, narrow coenosorus along the costa, deeply immersed in a central groove; lamina 0.5 cm. broad or less. *Cochlidium*.
- ddd. Sporangia arranged in linear or elongated sori, parallel or diagonal with the costa, or in indefinite patterns along the veins; lamina commonly 1 cm. or much broader.
- eee. Sporangia borne singly or in small clusters, sparsely scattered along (and sometimes between) the veins. *Anetium*.
- eee. Sporangia in definite, elongated to linear sori, or densely lining the veins in somewhat crooked or forked or reticulate patterns.
- fff. Areoles (at least some of them) with free, included veinlets. . . .
Loxogramme.
- fff. Areoles lacking free, included veinlets.
- ggg. Costa prominulous abaxially; paraphyses lacking.
Polytaenium.
- ggg. Costa plane or scarcely prominulous abaxially; paraphyses numerous, abruptly enlarged from a thin, pedicel-like base. .
Antrophyum.
- ccc. Leaves deeply lobed to pinnate or decompound, or if simple and entire then the sporangia grouped in roundish to oblong sori borne at definite points on the veins; lamina glabrous, pubescent, or scaly.
- hhh. Sporangia borne in lines, bands, or indefinite patterns along the veins, or nearly filling the fertile segments.
- iii. Leaves subflabellate and dichotomously lobed, or palmate to pinnatifid, without discrete pinnæ.
- jjj. Leaves dichotomously lobed, sessile, 1-3 cm. long; veins free. . .
Hecistopteris.

- jjj. Leaves typically palmate to pinnatifid, long-petiolate, 8-40 cm. long; veins copiously areolate. *Hemionitis*.
- iii. Leaves 1- to 5-pinnate, with pinnae discrete (sessile to long-stalked).
 - kkk. Sporangia in long, narrow, distinct, subparallel lines following the vein pattern; lamina terminating in a discrete, conform or subconform, apical segment, not farinose. *Gymnopteris*.
 - kkk. Sporangia in short bands or indefinite patterns, or in dense masses obscuring the segment surface; lamina not terminating in a conform or subconform apical segment, or if so, the abaxial surface conspicuously farinose.
 - lll. Leaves simply pinnate, indeterminate, with pinnae orbicular-cordate and strongly revolute. *Jamesonia*.
 - lll. Leaves 2- to 5-pinnate, or if simply pinnate the leaves determinate and the pinnae linear or linear-lanceolate.
 - mmm. Rhizome and petiole base amply to densely provided with broad scales.
 - nnn. Ultimate segments strongly reflexed, beadlike, often subbullate and almost completely covering the sporangia; lamina not farinose. *Plecosorus*.
 - nnn. Ultimate segments somewhat revolute, but never beadlike, scarcely protecting the sporangia; lamina commonly farinose. *Pityrogramma*.
 - mmm. Rhizome and petiole pubescent or glabrate, or if scaly, the scales few and filamentous.
 - ooo. Leaves delicate, 6-25 cm. long, 2-5 cm. broad, membranaceous; rhizome provided with fine, septate trichomes and a few filamentous scales. *Anogramma*.
 - ooo. Leaves rather coarse, 40-400 cm. long, 10-50 cm. broad, firm-herbaceous to subcoriaceous; rhizome provided with stout, bristle-like trichomes, scales lacking. *Eriosorus*.
- hhh. Sporangia arranged in discrete, roundish or oblong sori, these rarely confluent at maturity.
 - ppp. Ultimate segments conspicuously spinulose on the margins or apices. *Polystichum*.
 - ppp. Ultimate segments not spinulose.
 - qqq. Lamina 2-pinnate-pinnatifid to 4-pinnate.
 - rrr. Major axes furrowed adaxially, the furrow flanked by ridges which are continuous as ridges on the axes of the next order above or below. *Lastreopsis*.
 - rrr. Major axes plane to slightly furrowed adaxially, and if so the ridges not continuous onto the axes of the next order above or below. *Ctenitis*.
 - qqq. Lamina simple to pinnate-pinnatifid (very rarely 2-pinnate).
 - sss. Petiole articulate (sometimes obscurely so) to the rhizome or to the phyllopodia arising from it. *Polypodium*.
 - sss. Petiole not articulate.
 - ttt. Leaves simple or pinnatifid.
 - uuu. Veins copiously areolate, with free, included veinlets; petiole scaly (at least toward the base). *Tectaria*.

- uuu. Veins free, or rarely with a few areoles and then lacking free, included veinlets; petiole lacking scales.
Grammitis.
- ttt. Leaves pinnate or pinnate-pinnatifid.
- vvv. Lamina more or less pubescent with acicular, hamate or stellate trichomes; scales present or lacking.
Thelypteris.
- vvv. Lamina sparsely to amply scaly (at least on the axes), but lacking trichomes. *Stigmatopteris*.

ACROSTICHUM Linnaeus

Terrestrial plants of low, wet places, most commonly in mangrove swamps; rhizome stout, erect, woody, amply scaly at apex, amply provided with thick (to 7 mm.), spongy roots; leaves quite large, coarse, caespitose, petiolate, monomorphous or essentially so (fertile leaves occasionally somewhat longer and their pinnae slightly more constricted); petiole not articulate, stout and smooth, glabrous, terete to subquadrangular, adaxially sulcate; lamina pinnate, glabrous or minutely pubescent, firm-herbaceous to subcoriaceous, terminating in a conform (though sometimes reduced), stalked, apical segment, not or scarcely reduced at base, or occasionally with the basal 1-2 pairs of pinnae greatly reduced or merely persisting as spines; rachis smooth, glabrous, terete abaxially, flattened to sulcate adaxially; pinnae stalked, simple, spreading to strongly ascending; venation copiously areolate, the veins distinct and prominulous on both surfaces, the areoles subrectangular to hexagonal, lacking free, included veinlets; sporangia long-stalked, completely covering the abaxial surface, intermixed with abundant paraphyses; indusia lacking; spores trilete, tetrahedral, with perine.

The genus should be confused with no other in Guatemala. It is distinguished by the simply pinnate leaves, with the abaxial surfaces of the fertile pinnae completely covered by masses of sporangia. It is a tropical or subtropical fern of wet places, most commonly found in mangrove swamps, but sometimes found in the mud of lake shores or river banks. Two species occur in the neotropics, and perhaps two more in the Old World.

- a. Pinnae widely spaced; fertile lamina with only the distal pinnae bearing sporangia; paraphyses abruptly and conspicuously dilated, mostly capitate-stellate.

A. aureum.

- a. Pinnae (at least the distal ones) crowded to, more commonly, imbricate; fertile lamina with most pinnae bearing sporangia; paraphyses oblong or allantoid.

A. daneaeifolium.

Acrostichum aureum L. Sp. Pl. 1069. 1753.

In mangrove swamps, at sea level; Izabal; San Marcos; Petén. Southern Florida; West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Brazil and Peru; Old World tropics.

Rhizome scales rigid, several cells thick, 0.5-1.5 cm. long, numerous and closely packed, brown or bicolorous (with a blackish median stripe), linear to lanceolate, or older



FIG. 1. *Acrostichum*. a-b, *A. aureum*: a, apex of fertile lamina, $\times \frac{1}{2}$; b, venation pattern, $\times 6$; c-d, *A. daneaeefolium*: c, pinna, $\times \frac{1}{2}$; d, venation pattern, $\times 6$.

ones near the petiole base very broadly ovate with margins erose; leaves to 2 m. long (in ours); petiole yellow- or gray-brown, usually shorter than the lamina; lamina 15-40 cm. broad, glabrous, oblong or elliptic, fertile only toward the apex or, at most, in the distal half; pinnae 8-15 pairs, sharply ascending to (rarely) spreading, widely spaced, all but the distalmost stalked, larger ones 12-30 cm. long, 3-6 cm. broad, obtuse to subacute, broadly to sharply cuneate at base, lanceolate or narrow-oblong, margins entire and cartilaginous, sometimes slightly revolute; areoles aligned at 45-60° angles to the costa, the costal ones mostly long and narrow and oriented subparallel to the costa; paraphyses deep castaneous, numerous but minute (commonly only 2-3 times as large as the spores) borne on thin stalks, abruptly dilated at apex, most of them lobed- to stellate-capitate.

Acrostichum daneaefolium Langsd. & Fisch. Icon. Fil. 1: 5, *t.* 1. 1810. *A. excelsum* Maxon, Proc. Biol. Soc. Wash. 18: 224. 1905.

In mangrove swamps, marshes, or muddy banks of rivers or lakes, sea level to 1,200 m.; Escuintla; Guatemala; Izabal. Florida; West Indies; Mexico to Panama; Colombia to the Guianas, south to Bolivia and Paraguay.

Rhizome scales not seen; leaves to 3 m. long (in ours); petiole yellowish to reddish brown, usually much shorter than the lamina; lamina 20-60 cm. broad, glabrous adaxially, copiously but minutely pilose abaxially, oblong or elliptic, most pinnae (not just the distal ones) of fertile laminae bearing sporangia; pinnae numerous, sharply ascending to (rarely) spreading, stalked to (distally) adnate, the proximal ones widely spaced, the rest crowded to (more commonly) imbricate, broadly to sharply cuneate at base, obtuse to (more commonly) acute, lanceolate to narrow-elliptic, margins plane, entire, cartilaginous; areoles aligned at 60-90° angles to the costa, the costal ones as broad or broader than long, also mostly oriented obliquely or perpendicularly to the costa; paraphyses numerous, light or dark brown, small (but many times larger than the spores), mostly borne on thin stalks and oblong or allantoid, commonly crispate on dried specimens.

This and *A. aureum* are often difficult to separate as dried specimens, for the leaves are quite large, and few collectors include enough of the lamina to exhibit all of the diagnostic features. If only the central or proximal portions of lamina are mounted, the crowded to imbricate distal pinnae of *A. daneaefolium* will not be evident, or if only the distal portion of a fertile lamina is mounted, it may not be determined if the next, missing, pinnae are also fertile (*A. daneaefolium*) or sterile (*A. aureum*). In this case, two other characters, discerned even on a single sterile pinna, may be helpful.

On Guatemalan specimens (and on most of the others I have examined) leaves of *A. aureum* are glabrous, whereas in *A. daneaefolium* the abaxial surface is minutely but amply strigose. Some authors have attempted to separate the two species on the angle at which the areoles are aligned on the pinnae. I have not found this to be consistent enough throughout the breadth of the pinnae, but it appears to be an

effective character when applied strictly to the *costal* areoles; *i.e.*, those of *A. daneaefolium* are broad and mostly spreading obliquely from or perpendicular to the costa. In *A. aureum* most of the basal veins spring from the costa and run alongside it before merging with the adjacent vein, or often simply rejoining the costa—in any case, the areoles thus formed are long and narrow and are oriented parallel to the costa.

ADENODERRIS J. Smith

REFERENCE: W. R. Maxon, *Adenoderris*, a valid genus of ferns, Bot. Gaz. 39: 366-369. 1905.

Plants small, terrestrial, commonly growing among rocks or in rock crevices; rhizome short, relatively stout, erect, provided with glandular scales; leaves fasciculate, commonly less than 15 cm. long, deeply pinnatisect to pinnate-pinnatifid, not articulate; lamina herbaceous, glandular-pilose; venation anadromous, the veins free, commonly 1- to several-forked, reaching the segment margin or (in ours) terminating short of the margin; sori abaxial on the segments, borne along the veinlets or (in ours) at the tips of veinlets, circular, partially covered by a peltate indusium; sporangia long-stalked; spores dark brown, monolete, roughly oblong, with perine, lightly tuberculate.

The genus contains two species, *A. viscidula* (Mett.) Maxon of Cuba and Jamaica, and *A. sororia* of Guatemala. Both are small, inconspicuous species, apparently confined to rocky habitats.

Adenoderris sororia Maxon, Bot. Gaz. 39: 368. 1905.

Known only from the type, collected in rock crevices along river, in "Sesisp" (perhaps Sesibché, one of the caserios in San Pedro) between San Pedro Carcha and Senahú, Alta Verapaz, 900 m., *Tuerckheim* (ed. *Donn.-Sm.* No. 868).

Rhizome short, erect, provided with light-brown, lanceolate scales, these appearing ciliate, with minute glands along their margins; leaves several, to 8 cm. long and 2.5 cm. broad; petiole 0.5-1.5 cm. long, stramineous, subterete, often marginate or very narrowly winged for part of its length, provided with scales as on the rhizome, and with abundant, minute, gland-tipped trichomes; lamina herbaceous, lanceolate to oblanceolate, minutely glandular throughout, pinnate-pinnatifid, narrowing to a pinnatifid apex, slightly reduced at base; pinnae 5-12 pairs, sessile or subsessile, lobed more than halfway to a flexuous costa, the basal acroscopic lobe much the largest; veins simple or 1-forked (or several-forked in largest basal lobes), not reaching the margin; sori commonly 1 to a lobe, terminal on the veinlets, each commonly containing 6-12 sporangia; indusium peltate, orbicular, minutely glandular.

Nearly 100 years have passed since the type of *A. sororia* was first collected, and evidently it has not been reported since. From its Antillean counterpart it differs in its shorter stature, less glandular leaves, deeply lobed pinnae, and sori which are terminal on the simple



FIG. 2. *Adenoderris sororia*. a, habit, full size; b, pinna, $\times 2\frac{1}{2}$; c, indusium, abaxial view and cross-section, greatly enlarged.

to 1-forked veins. *Adenoderris viscidula* has pinnae subentire to crenate, and sori which are borne along the several-forked veins.

ADIANTUM Linnaeus

REFERENCES: R. M. Tryon, *Adiantum*, in: *The ferns of Peru—Polypodiaceae*, Contr. Gray Herb. 194: 135-180. 1964; G. R. Proctor, in: Howard, *Flora of the Lesser Antilles*, Vol. 2, Pteridophyta, Jamaica Plain, Mass, pp. 179-192. 1977.

Plants terrestrial (but frequently in very rocky situations); rhizome long- or short-creeping to suberect, scaly, the scales commonly minute, narrow, obscurely or not at all clathrate, the margins sometimes setulose to short-ciliate; leaves small to over 1 m. long, essentially monomorphic (although the fertile ultimate segments occasionally are somewhat constricted), long-petiolate; petiole not articulate, glabrous, scurfy, pubescent or scaly, terete or flattened to quadrangular, lustrous, dark brown to (more commonly) atropurpureous or blackish; lamina pinnate to 5-pinnate (rarely subpedate and the branches helicoid or, more rarely, simple), often glaucous abaxially, glabrous to minutely pubescent or filiform-scaly, firm-herbaceous to subcoriaceous, typically broad (often as broad or broader than long), tapering gradually to a pinnatifid apex, or terminating in a conform, pinnalike apical segment; ultimate segments commonly dimidiate or subflabellate, sometimes articulate and deciduous; venation free or (very rarely) anastomosing, the veins dichotomously branched, their tips reaching the segment margin and (on fertile segments) into the indusia; sori essentially marginal, short and dis-

crete, or long and continuous (sometimes from base to apex of the segments); indusium thin to quite firm, composed of a modified, reflexed, marginal flap or lobe which may be (like the sorus) discrete or long and uninterrupted; paraphyses lacking; sporangia slender-stalked, borne between and/or on the tips of veins on the underside of the indusium; spores trilete, tetrahedral, perine very thin or lacking.

Adiantum is a pantropical genus of nearly 200 species, including a few in temperate areas. It is one of the most easily recognized of all fern genera, because of its usually inequilateral segments, its dark-colored, highly lustrous petioles, and the distinctive modified, marginal flaps which serve as indusia. There are a few other genera with similar indusia, but none in which the veins actually extend into these flaps.

The genus contains many species of great beauty and delicacy, which therefore are quite popular for purposes of cultivation. Some of these in tropical regions respond so well that they readily escape and have become naturalized. The popular name for many of the species is "culantrillo" ("maidenhair" fern).

- a. Lamina simply pinnate, or very rarely the basal pair of pinnae again pinnate.
 - b. Pinnae commonly with 1, long, nearly continuous sorus on each margin; dark color of pinna stalk passing well into the base of the segment.
 - c. Pinnae 3-7 pairs, mostly opposite or subopposite, with costa lacking, or discernible only at pinna base; veins free. *A. macrophyllum*.
 - c. Pinnae 1-2 (3) pairs, alternate, with costa distinct nearly throughout; veins (several to many) anastomosing. *A. wilsonii*.
 - b. Pinnae with several to many short sori on each margin; dark color of pinna stalk scarcely or not at all passing into base of segment.
 - d. Pinnae conspicuously stalked throughout the lamina.
 - e. Lamina coarse; pinnae ovate-acuminate, 5-15 cm. long and 1.5-8 cm. broad. *A. seemannii*.
 - e. Lamina delicate; pinnae flabellate to lunate or oblong-lunate, rarely over 3 cm. long and 1.5 cm. broad.
 - f. Margins of sterile pinnae denticulate; pinna stalks abruptly dilated at segment base, the dark color ending in a sharp, even line. *A. deflexens*.
 - f. Margins of sterile pinnae entire to crenulate; pinna stalks not or scarcely dilated, the dark color line irregular. *A. lunulatum*.
 - d. Pinnae sessile to subsessile, or a few proximal ones short-stalked.
 - g. Pinnae somewhat lustrous on both surfaces, the margins of sterile ones irregularly biserrate and often shallow-crenate. *A. obliquum*.
 - g. Pinnae glaucous abaxially, the margins of sterile ones regularly and finely serrulate. *A. petiolatum*.
- a. Lamina decompose.
 - h. Leaf subpedate, *i.e.*, forked at petiole apex, with pinnalike divisions successively produced along the acroscopic side of each fork. *A. patens*.
 - h. Leaf with a normal rachis, this bearing pinnae regularly and alternately throughout its length.

- i. Ultimate segments (most of them) conspicuously stalked.
- j. Stalks of ultimate segments each bearing a whitish callus at juncture with next axis below (calluses usually present in axils of other axes as well). . . . *A. braunii*.
- j. Stalks of ultimate segments (and other axes) lacking whitish calluses.
- k. Pinnae commonly 15-24 pairs, sessile; basal acroscopic pinnule forked and greatly reduced (at least on proximal pinnae), borne about 1 mm. from, and conspicuously overlapping, the rachis. *A. concinnum*.
- k. Pinnae 4-14 (-16) pairs, stalked; basal pinnules commonly pinnate and well-developed, not particularly crowding the rachis.
- l. Dark color of stalk commonly entering the ultimate segment, or if not, then gradually and irregularly blending with the lighter color of the costa or veins.
- m. Margins of sterile segments sharply and regularly dentate or denticulate, the vein tips each ending in a tooth; rhizome scales often distinctly clathrate, especially at base. *A. capillus-veneris*.
- m. Margins of sterile segments entire to denticulate or crenate, the vein tips each ending in a sinus (where present); rhizome scales not or obscurely clathrate.
- n. Sori oblong, oblong-lunate, or subreniform, the sinus broad and shallow or nearly lacking. *A. poiretii*.
- n. Sori orbicular-reniform, the sinus very narrow, often deep.
A. raddianum.
- l. Dark color of stalk abruptly terminating at base of ultimate segment, or if briefly entering the segment base then abruptly and markedly contrasting with the lighter color of costa and/or veins.
- o. Ultimate segments (and often their stalks) pubescent at least abaxially.
- p. Rachis hispidulous (often densely so); minor axes densely hispidulous, the trichomes very short and thick and often nearly covering the axis; plants growing at 1,200-2,300 m. altitude. *A. feei*.
- p. Rachis essentially glabrous; minor axes sparsely pilose, the trichomes long and slender, scattered; plants growing at 50-200 m. altitude. . .
A. tricholepis.
- o. Ultimate segments and stalks glabrous.
- q. Ultimate segments conspicuously articulate at base, sharply and cleanly deciduous, the stalk abruptly dilated at its apex, leaving a thin, flat disk where the segment has fallen away.
- r. Rhizome scales 3-6 mm. long, light brown to orange, concolorous, the margins setulose; ultimate segments with sterile portion of margin entire, crenulate, or (rarely) broadly and obscurely denticulate. *A. princeps*.
- r. Rhizome scales 0.5-2 mm. long, castaneous to blackish, mostly with a thin, light-brown or scarious, ciliate or ciliolate margin; ultimate segments with sterile portion of margin sharply and conspicuously dentate or denticulate. *A. tenerum*.
- q. Ultimate segments not articulate, not or irregularly deciduous, the stalk scarcely or not at all dilate, but leaving an irregular fracture line where segment has fallen away.
- s. Larger ultimate segments 1-2 (2.5) cm. long, mostly obovate or subflabellate; lamina 3- to 5-pinnate, with (6) 7-12 pairs of pinnae, and tapering gradually to the apex. *A. andicola*.

- s. Larger ultimate segments 4-7 cm. long, trapeziform, ovate, or lanceolate; lamina 2-pinnate (or 3-pinnate as to basal pinnae), with 2-4 pairs of pinnae and a similar apical segment.
- t. Rachis and/or costae sparsely provided with filiform scales; ultimate segments ovate to lanceolate (or a few trapeziform), larger ones with a light-colored midrib evident in the basal half, abaxially. *A. caryotideum*.
- t. Rachis and costae lacking scales; ultimate segments (most of them) trapeziform, lacking a midrib. *A. trapeziforme*.
- i. Ultimate segments sessile or subsessile, the stalks (if any) relatively very short (rarely over 1 mm.) and inconspicuous.
 - u. Pinnae commonly 15-24 pairs, sessile; basal acroscopic pinnule forked and greatly reduced (at least on proximal pinnae), borne about 1 mm. from, and conspicuously overlapping, the rachis. *A. concinnum*.
 - u. Pinnae (1) 2-10 pairs, short-stalked to subsessile; basal acroscopic pinnule simple to 2-pinnate, not forked, often touching, but not overlapping, the rachis.
 - v. Rachis and costae glabrous, or minutely puberulent with simple trichomes not more than 0.1 mm. long; pinnae (at least the basal pair) 2-pinnate or 3-pinnate.
 - w. Rachis and costae glabrous; indusium commonly plane and squarish or semicircular (sometimes broadly oblong). *A. polyphyllum*.
 - w. Rachis and costae densely puberulent abaxially; indusium convexly enveloping the developing sporangia, mostly allantoid. . . . *A. wilesianum*.
 - v. Rachis and costae scaly, the scales often hairlike, 0.5-4 mm. long; pinnae 1-pinnate.
 - x. Rachis scales mostly 2-4 mm. long and spreading, highly lustrous, castaneous. *A. decoratum*.
 - x. Rachis scales 0.5-1.5 (2) mm. long, commonly subappressed, dull or scarcely lustrous, tan to medium brown (except often dark brown in *A. pulverulentum*).
 - y. Margins of sterile pinnules evenly serrate or serrulate; sori (1 or 2 of them) commonly borne along the acroscopic base of pinnules (parallel to the costa); lamina slightly to strongly glaucous abaxially.
 - z. Pinnules (larger ones of lateral pinnae) 2-4 cm. long, glabrous or with a few, scattered, hairlike scales along the veins abaxially; lamina with the pinnalike apical segment not or scarcely reduced at base.
 - A. latifolium*.
 - z. Pinnules rarely reaching 2 cm. in length, abundantly castaneous-pilose abaxially; lamina with the pinnalike apical segment strongly reduced at base. *A. terminatum*.
 - y. Margins of sterile pinnules coarsely and irregularly serrate or crenate-serrate; sori never (or very rarely) borne along the acroscopic base of pinnules; lamina not glaucous.
 - aa. Pinnules nearest the apical segment not very strongly reduced, the ultimate pair about $\frac{1}{2}$ as long as the larger, central ones; ultimate segments commonly with a definite (though often indistinct) midrib extending nearly to the apex; apical segment of fertile pinnae frequently bearing sori. *A. villosum*.

- aa. Pinnules gradually and very strongly reduced toward pinna apex; ultimate segments with midrib lacking, or present (and barely perceptible) only near the apex; apical segment of pinnae rarely or never bearing sori.
- bb. Ultimate segments bearing 1 long, continuous sorus along the acroscopic margin, rarely with a short one adjacent to it and a single short one at the apex. *A. pulverulentum*.
- bb. Ultimate segments bearing 4-7 short, discrete sori on the acroscopic margin and 1 (2) at the apex. *A. tetraphyllum*.

Adiantum andicola Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. V. 1: 266 (seors. 114). 1849. *A. glaucophyllum* Hook. Sp. Fil. 2: 40. 1851.

Very common species, in forests, thickets, and wooded ravines, frequently on shaded slopes or rocky banks, 1,000-3,400 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Jalapa; Jutiapa; Petén; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Suchitepéquez; Totonicapán. Mexico to Colombia and Venezuela.

Plants terrestrial; rhizome short- to long-creeping or ascending, provided with castaneous to blackish, mostly appressed, scales, these 1-2 mm. long, thick, rigid, often convexoconcave and with a subulate tip, not clathrate; leaves approximate to subfasciculate, 30-70 cm. long, 15-32 cm. broad, petiolate; petiole 15-40 cm. long, about as long as the lamina, stout, 1-2.5 mm. thick, terete, lustrous, castaneous to atropurpureous, sometimes somewhat glaucous, glabrous, but often with a few brown, spreading scales near the base; lamina firm-herbaceous to chartaceous, glabrous, often somewhat glaucous abaxially, 3- to 5-pinnate, deltoid; rachis lustrous, glabrous; pinnae stalked, (6) 7-12 pairs; ultimate segments 0.8-2 (2.5) cm. long, cuneate, obovate, cuneiform, or subflabellate, most of them lobed to deeply lacerate, with sterile portions of the margin sharply dentate or denticulate (or rarely subentire), long-stalked, the stalks not or slightly dilated, not articulated at the apex, castaneous to atropurpureous, the dark color abruptly terminating at base of segment, sharply contrasting with the lighter color of the veins; veins free, subflabellate, and several times forked, the tips ending in the marginal teeth; sori several on each ultimate segment, usually solitary on a segment lobe, elongate- to suborbicular-reniform, with the sinus broad and rounded, or often lacking; indusium rather thick and coarse, but often greatly constricted at maturity, joined with the margin proper in a concave to nearly straight line.

This is perhaps the most common species of *Adiantum* in Guatemala, having been collected thus far in all but seven departamentos. It may be readily distinguished from similar species by the highly dissected (3- to 5-pinnate) leaves, the small, rigid, often convexoconcave and subulate-tipped rhizome scales, the small, cuneate segments with the dark color of the stalks ending short of the segment base, and the veins mostly ending in the teeth of sterile margins.

***Adiantum braunii* Mett. ex Kuhn, Linnaea 36: 75. 1869.**

In forests, thickets, and wooded ravines, 1,200-2,000 m.; Guatemala; Huehuetenango; Sacatepéquez. Mexico; Costa Rica; Colombia.

Plants terrestrial; rhizome short- or long-creeping, provided with linear-lanceolate to filiform scales, these 1-2 mm. long, dark brown, blackish, or bicolorous (black at base or center, with narrow brown margins); leaves approximate to crowded, 30-90 cm. long, 15-30 cm. broad, petiolate; petiole 12-45 cm. long, shorter than or equaling the lamina, stout, 0.8-2.2 mm. thick, terete, lustrous, castaneous to atropurpureous, glabrous, but often with a few, spreading brown scales near the base; lamina thin- to firm-herbaceous, glabrous, often shiny-glandular, 2- to 3-(4-) pinnate, deltoid; rachis lustrous, glabrous; pinnae stalked, 7-12 pairs, often bearing whitish, callous spots in the axils along rachis and costae; ultimate segments obovate, subflabellate, or broadly oblong, shallowly to deeply lobed, or undivided, entire to faintly crenulate, fertile ones commonly somewhat constricted and smaller than the sterile, long-stalked, the stalks not dilated or articulated at segment base, castaneous to atropurpureous, the dark color not or scarcely entering the segment base, a whitish, callous spot borne at base of stalk; veins free, subflabellate, and several times forked, the tips running to the slightly thickened margin; sori several to a segment, 1 or 2 on each of the lobes, oblong to allantoid; indusium thick and coarse, joined with the margin proper in a straight or concave line.

This is a rather uncommon plant, with disjunct distribution from Mexico to Colombia. Its affinities are with *A. andicola* and *A. poiretii*, but it is easily distinguished from both by the conspicuous, whitish, callous spots which occur at the base of each segment stalk at the juncture with the axis of the next order below. Such calluses are commonly found in the axils of other axes as well, although these may not be quite so conspicuous.

***Adiantum capillus-veneris* L. Sp. Pl. 1096. 1753.**

In forests and wooded ravines, on wet banks of ravines and along rivers and streams; also found cultivated in gardens, 1,100-2,400 m.; Alta Verapaz; Chimaltenango; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá. Southern United States; Mexico; West Indies; Venezuela; Peru; tropical and temperate areas of the Old World.

Plants terrestrial; rhizome creeping, provided with amber to castaneous, linear to broadly lanceolate scales, these 1-2 mm. long, entire, rather distinctly clathrate, at least at the broadened base; leaves approximate, 15-35 cm. long, 3-10 (12) cm. broad, petiolate; petiole 6-16 cm. long, commonly shorter than the lamina, wiry, 0.5-1.8 cm. thick, flattened to sharply angled, sulcate, lustrous, castaneous to atropurpureous, sometimes somewhat glaucous, glabrous, but with a few scattered scales toward the base; lamina delicate, membranaceous to firm-herbaceous, commonly 2-pinnate, or sometimes 3-pinnate in the proximal portion, ovate to elongate-deltoid; rachis lustrous, glabrous; pinnae stalked, 6-9 pairs, glabrous, most of them with 2-6 pairs of pinnules; ultimate segments cuneate, subflabellate to obovate or nearly circular, often deeply cleft, with the sterile portions of the margin sharply dentate or denticulate, long-stalked, the stalks

not dilated nor articulated at the apex, castaneous to atropurpureous, the dark color commonly entering the segment and then gradually blending with the lighter color of the veins; veins free, subflabellate, and 2-3 times forked, the tips ending in the marginal teeth; sori few on each ultimate segment, usually solitary on a segment lobe, oblong or lunate, the indusium joined with the margin proper in a straight or concave line.

Adiantum caryotideum Christ, Bull. Soc. Bot. Genève II. 1: 230. 1909.

In forests or thickets, usually along the banks of rivers or streams, 300-400 m.; rare, Retalhuleu. Mexico (Chiapas); Costa Rica; Panama.

Plants terrestrial; rhizome short-creeping, woody, amply provided with linear or lanceolate scales, these 1-2 mm. long, castaneous, scarcely or not clathrate; leaves crowded to approximate, 50-90 cm. long, 18-28 cm. broad, long-petiolate; petiole 23-50 cm. long, commonly longer than the lamina, wiry or stout, 1.5-2.5 cm. thick, terete, or flattened to shallow-sulcate adaxially, lustrous, atropurpureous to blackish, sparsely filiform-scaly or glabrate; lamina essentially glabrous, though usually glaucous abaxially, thin- to firm-herbaceous, deltoid, 2-pinnate, with 2-4 pairs of stalked pinnae and a similar (usually somewhat longer) terminal segment; rachis and costae atropurpureous to blackish, lustrous, sparsely provided with brown, filiform scales about 1 mm. long; ultimate segments 2.5-7 cm. long, lanceolate to ovate, inequilateral at base, acroscopically truncate, basiscopically excavate, irregularly biserrate (except along the truncate or excavate basal portion), stalked, the stalks sparsely filiform-scaly, atropurpureous or blackish, the dark color not or scarcely entering the segment and then abruptly and markedly contrasting with the midrib and veins, a midrib evident (abaxially) at least in the basal half of larger segments; veins free, subflabellate, or obliquely arising from the midrib, several times forked, the tips ending in the marginal teeth; sori 5-6 along the acroscopic margin (fewer basiscopically), linear or narrow-oblong; indusium brown, rather thin, commonly withering and inconspicuous at maturity.

This is a rare fern, confined to Central America, and is thus far represented by only two collections in Guatemala. It can be easily confused with *A. trapeziforme*, which it resembles in size and architecture of leaf. Besides the characters used in the key, *A. caryotideum* may be distinguished by the fewer sori (commonly only 5-6 to a segment acroscopically—less basiscopically) and the thin indusia which usually soon shrivel and are thus inconspicuous at maturity. Sori are much smaller and more numerous in *A. trapeziforme* (often 12-16 on the acroscopic margin), and the indusia are coarse and generally persistent, even at maturity.

Adiantum concinnum H. & B. ex Willd. in L. Sp. Pl. 5: 451. 1810.

In forests, thickets, and wooded ravines, often on the faces of cliffs or rocky banks, or along streams and rivers, 300-2,000 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; Jutiapa; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Suchitepé-

quez; Zacapa. West Indies; Mexico to Panama; Colombia; Venezuela; Brazil; Ecuador; Peru.

Plants terrestrial; rhizome short-creeping, stout, provided with orange to castaneous, linear or lanceolate scales, these 2-4 mm. long, entire, scarcely or not at all clathrate; leaves subcaespitose, sometimes pendent, 30-55 cm. long, 6-18 cm. broad, petiolate; petiole 8-20 cm. long, shorter than the lamina, wiry or stout, 0.5-1.8 mm. thick, terete or slightly flattened, lustrous, castaneous to atropurpureous, glabrous; lamina delicate, glabrous, membranaceous to firm-herbaceous, 2-pinnate to 3-pinnate, ovate to linear-lanceolate; rachis lustrous, glabrous; pinnae sessile, commonly 15-24 pairs, glabrous, most of them with 4-8 pairs of pinnules, the basal acroscopic pinnule (at least on proximal pinnae) commonly forked and greatly reduced, borne about 1 mm. from, and conspicuously overlapping, the rachis; ultimate segments subflabellate to obovate, often deeply cleft, with the sterile portions of the margin subentire or crenate to obscurely dentate, short-stalked, the stalks not dilated or articulated at apex, castaneous to atropurpureous, the dark color entering the segment, or at least blending gradually with the lighter color of the veins; veins free, subflabellate, and 2- to 3-forked, the tips each ending in a sinus (where a sinus is present); sori few on each ultimate segment, usually solitary on a segment lobe, suborbicular-reniform, the sinus very deep and narrow.

***Adiantum decoratum* Maxon & Weath. Amer. J. Bot. 19: 165. 1932.**

In wet forests, often along river banks, sea level to 350 m.; Alta Verapaz; Izabal; Petén; Retalhuleu. Mexico; Honduras; Nicaragua; Costa Rica; Panama; Colombia.

Plants terrestrial; rhizome stout, woody, short-creeping, amply provided with linear or filiform, castaneous scales, 1-3 mm. long; leaves densely crowded, 40-70 cm. long, 20-28 cm. broad, petiolate; petiole 20-40 cm. long, about as long as the lamina, lustrous, atropurpureous, terete to quadrangular, densely scurfy and scaly, the scales lustrous, castaneous, spreading, filiform, 2-4 mm. long; lamina firm-herbaceous to chartaceous, leaf tissue glabrous, commonly glaucous abaxially, 2-pinnate, with 5-9 pairs of pinnae and a similar apical segment, this somewhat (but not greatly) reduced at apex and base; rachis lustrous, this and the costae densely scurfy and scaly as on the petiole; pinnae subsessile or short-stalked, terminating rather abruptly in a lanceolate apical segment; pinnules mostly 1-2.2 cm. long, obtuse, dimidiate, lacking a midrib, those near the base and apex of pinnae somewhat (not strongly) reduced, about $\frac{1}{2}$ the length of the longest central ones, the acroscopic margin and apex of sterile segments finely and regularly serrate or serrulate; veins free, subflabellate, and 2- or 3-forked, the tips each ending in a marginal serration; sori short, discrete, commonly confined to the proximal half of pinnae (never on the apical segment), 4-7 along the acroscopic margin of pinnules, and usually 1-2 at the apex; indusium rather thick, joined with the margin proper in a straight or concave line.

***Adiantum deflectens* Mart. Icon. Pl. Crypt. Bras. 94. 1834.**

In forests or wooded ravines, on forest floor or on clay or rocky banks or cliffs, 250-600 m.; Chiquimula; Zacapa. Honduras; El Salvador to Panama; Colombia to the Guianas, south to Peru, Brazil, and Paraguay.

Plants terrestrial or epipetric; rhizome short-creeping to ascending, provided with linear, castaneous to blackish scales, these about 1 mm. long, rather rigid, not or scarcely clathrate, with margins subentire; leaves subcaespitose, 10-32 cm. long, 2-4 cm. broad, petiolate; petiole 2-10 cm. long, shorter than the lamina, wiry, 0.2-0.7 mm. thick, terete to flattened, often narrow-sulcate adaxially, lustrous, castaneous to atropurpureous, essentially glabrous but with a few scattered scales toward the base, like those of the rhizome except longer and often bicolorous (blackish, with margins lighter-colored); lamina delicate, membranaceous, simply pinnate, linear to elongate-triangular, with a subconform, apical segment, or lacking an apical segment and terminating in a flagelliform, radicate tip; rachis glabrous, lustrous, castaneous to atropurpureous; pinnae 4-12 pairs, 1.5-2.5 cm. long, 0.8-1.5 cm. broad, glabrous, lunate, or (most commonly) flabellate and cuneate, often deeply cleft into 2-6 lobes and with the sterile portions of the margin sharply denticulate, long-stalked, the stalks atropurpureous to blackish, abruptly dilated at the articulation with the pinna, the dark color sharply and regularly distinct (usually in a straight line) from the pinna base; veins distinct, free, several-times forked, radiating from the pinna base, the tips each ending in a marginal tooth; sori commonly 3-7, 1 to a pinna lobe, linear to oblong, straight or concave.

With this probably should be included *A. dolabriforme* Hook., of South America, and perhaps even *A. delicatulum* Mart. of Brazil, the latter described by Martius in the same publication at the same time as *A. deflectens*.

The only Guatemalan *Adiantum* possibly to be confused with *A. deflectens* is *A. lunulatum*. Besides the differences noted in the key, often the two may be distinguished by the shape of pinnae. The typical pinna in *A. lunulatum* is lunate or oblong-lunate, i.e., the proximal margins meet at the stalk in a straight or nearly straight line. Pinnae in *A. deflectens* are occasionally lunate, but most commonly they are flabellate, with proximal margins sharply cuneate to the stalk.

Adiantum feei Moore ex Fée, Mém. Fam. Foug. 7: 29, t. 24, f. 1. 1857 (type from Orizaba, Mexico, Schaffner 446). *A. flexuosum* Hook. 2d Cent. Ferns, t. 61. 1861 (type from Santa Rosa, Baja Verapaz, Salvin 464).

In open forests, on dry banks and slopes, and on dry, rocky hills, 1,200-2,300 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; El Progreso; Zacapa. Southern Mexico.

Plants terrestrial; rhizome erect or ascending, provided with castaneous to blackish, linear or lanceolate scales, these 1-2 mm. long, rigid, not clathrate; leaves subcaespitose, 40-130 cm. long, 12-35 cm. broad, petiolate; petiole 16-70 cm. long, equaling or shorter than the lamina, rather stout, 0.8-2.8 cm. thick, terete, lustrous, castaneous to atropurpureous, puberulent or glabrate; lamina firm-herbaceous to chartaceous, commonly 3- to 4-pinnate, ovate or deltoid-ovate; rachis lustrous, slightly to strongly flexuous, hispidulous (often densely so); pinnae stalked, widely spaced, ascending to spreading, or reflexed, 8-14 (16) pairs, costae and other axes densely brown-hispidulous; ultimate segments commonly 0.4-1.5 cm. long, amply white-pilous abaxially, broadly ovate to

obovate or circular, entire to broadly crenate or shallowly lobed, stalked, the stalks not dilated at apex, densely hispidulous, castaneous to blackish, the dark color terminating abruptly at the base of the segment; veins free, subflabellate, 2- or 3-forked, sori few on each segment, oblong to semicircular, or occasionally broadly reniform, the indusia brownish, firm, pilosulous.

***Adiantum latifolium* Lam. Encycl. 1: 43. 1783.**

In forests, thickets, and wooded ravines, frequently on banks of streams and rivers, occasionally in unshaded, roadside ditches, sea level to 300 m.; Alta Verapaz; Izabal; Petén; San Marcos; Santa Rosa. West Indies; Mexico to Panama; South America.

Plants terrestrial; rhizome long-creeping, amply provided with linear, acuminate scales, these 1-2 mm. long, castaneous, narrowly and obscurely clathrate; leaves approximate to well-spaced, 35-70 cm. long, 20-30 cm. broad, petiolate; petiole 18-42 cm. long, equaling or longer than the lamina, lustrous, castaneous, atropurpureous, or blackish, commonly quadrangular, amply scaly and scurfy; lamina 2-pinnate, with (1) 2-4 pairs of pinnae and a similar apical segment, this scarcely or not at all reduced at base, leaf tissue thin- to firm-herbaceous, adaxially green, abaxially slightly to strongly glaucous, glabrous or, rarely, with a few scattered, minute hairlike scales along the veins abaxially; rachis and costae scaly, the scales tan to medium brown, not or slightly lustrous, mostly appressed, filiform, 0.5-1.5 mm. long, with margins essentially entire; pinnae short-stalked to subsessile, terminating rather abruptly in an ovate or lanceolate apical segment; pinnules (larger ones of lateral pinnae) 2-4 cm. long, sessile or subsessile, dimidiate at base (truncate acroscopically, sharply cuneate or excavate basiscopically), subequilateral distally, with a definite, often indistinct, midrib running partly or most of the way to the obtuse or acute apex, sterile ones finely and regularly serrate or serrulate, those nearest the apical segment not greatly reduced (usually about $\frac{1}{2}$ the size of the larger, central ones); veins free, 1- or 2-forked, diverging from the midrib at a very narrow angle, the tips each terminating in a marginal serration; sori discrete, commonly borne from base to apex of pinna (although occasionally the apical segment sterile), 6-12 along the acroscopic margin, 3-6 on the basiscopical, and commonly 1-2 on the acroscopic base (parallel with the costa); indusium joined with the margin proper in a straight or concave line.

This is closely related to *A. serrato-dentatum* Willd., which is found in South America and parts of Central America. Indeed, a few specimens of *A. latifolium* and *A. terminatum*, from Guatemala and British Honduras, have been so named in various herbaria. *Adiantum serrato-dentatum* has the slender, long-creeping rhizomes and finely serrate segment margins of *A. latifolium*, but leaves of the former are much coarser, usually coriaceous, and are not glaucous.

***Adiantum lunulatum* Burm. f. Fl. Indica 235. 1768 (not Houtt. 1783). *A. philippense* L. Sp. Pl. 1094. 1753 (*sp. dub.*) *Pteris lunulata sensu* Roxb. Calcutta J. Nat. Hist. 4: 506. 1844.**

In forests, thickets, or wooded ravines, most commonly in rocky soil, on banks of streams and rivers, 200-1,500 m.; Huehuetenango;



FIG. 3. *Adiantum* (simply pinnate species). a, *A. macrophyllum*, habit, $\times \frac{1}{2}$; b, *A. deflectens*, pinna, $\times 3$; c, *A. lunulatum*, pinna, $\times 3$; d, *A. seemannii*, pinna, $\times \frac{1}{2}$; e, *A. petiolatum*, part of rachis with pinnae, $\times \frac{1}{2}$.

Retalhuleu; Santa Rosa. Cuba; Mexico; El Salvador; Nicaragua; Costa Rica; Panama; Colombia; Old World tropics.

Plants terrestrial; rhizome erect or ascending (rarely very short-creeping), provided with linear or lanceolate, castaneous to blackish (or bicoloured) scales, these 1-2 mm. long, rather rigid, not or scarcely clathrate, with margins subentire; leaves caespitose, 14-40 cm. long, 2.5-7 cm. broad, petiolate; petiole 4-16 cm. long, shorter than the lamina, wiry to stout, 0.4-1.4 cm. thick, terete to flattened, sulcate adaxially, lustrous, castaneous to atropurpureous, essentially glabrous, but with a few, scattered scales toward the base, similar to those of the rhizome; lamina delicate, membranaceous, simply pinnate, linear to elongate-triangular, with a subconform apical segment, or lacking an apical segment and terminating in a flagelliform, radicant tip; rachis glabrous, lustrous, castaneous to atropurpureous; pinnae 6-15 pairs, 1.5-3 (4) cm. long, 0.8-1.5 cm. broad, glabrous, lunate or oblong-lunate, often shallowly or deeply cleft into 3-7 irregular lobes, the sterile portions of the margin entire or crenulate, long-stalked, the stalks orange-brown to castaneous (in ours) or atropurpureous, not or scarcely dilated and not cleanly articulated at the pinna base, the dark color irregularly merging into the lighter color of the pinna base; veins distinct, free, several times forked, radiating from the pinna base, the tips reaching the margin; sori commonly 3-7, linear to oblong, straight or concave.

I am following Verma (Nova Hedwigia 3: 463. 1961) and Morton (Contr. U.S. Natl. Herb. 38: 370. 1974) in adopting the name *A. lunulatum* over that of *A. philippense*. The latter name was based only on a scarcely identifiable drawing of Petiver. See discussions by these authors for detailed explanations.

Adiantum lunulatum is most closely related to *A. deflectens*, under which see further comparison. Copeland (Fern Fl. Philipp. 1: 160. 1958) suggests it is probably introduced in the New World. If so, it has certainly become naturalized, as evidenced by its current distribution.

***Adiantum macrophyllum* Sw. Nov. Gen. Sp. Pl. Prodr. 135. 1788.**

In forests and thickets, often on wet banks of ravines, 80-1,800 m.; Alta Verapaz; Escuintla; Petén; Quezaltenango; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa. Greater Antilles; Martinique; Guadeloupe; Trinidad & Tobago; Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia; Galapagos Islands.

Plants terrestrial; rhizome short-creeping, densely covered with golden-tomentose roots and at apex provided with lustrous, castaneous scales, these 2-3 mm. long, filiform, or linear-lanceolate with acicular tips; leaves approximate to crowded, or subcaespitose, 30-70 cm. long, 8-16 cm. broad, long-petiolate; petiole 12-45 cm. long, as long or longer than the lamina, rather stout, 0.8-3 mm. thick, terete to flattened or angular, lustrous black or atropurpureous, sometimes slightly glaucous, glabrous; lamina glabrous, papyraceous to chartaceous, often glaucous abaxially, simply pinnate, with 3-7 pairs of pinnae and a similar, stalked, apical segment; rachis lustrous, black or atropurpureous, glabrous; pinnae (4) 5-10 cm. long, 2.5-5.5 cm. broad, opposite or subopposite, rhomboid, deltoid, or deltoid-ovate, truncate, broadly cuneate or rounded at the often inequilateral base, the sterile margins broadly and irregularly crenate or shallowly lobed (the lobes

sometimes serrulate), subsessile or very short-stalked, the dark color of the stalks passing distinctly into the bases of segments abaxially; costa lacking, or indistinct and discernible only in the basal portion of the segment abaxially; veins free, obscure or indistinct, several-forked, extending to the margin; 1 long sorus (rarely 2-3 more short ones) along each margin.

Leaf texture varies widely in this species, determined usually by maturity of the plant. In some young leaves the pinnae are so delicate and thin as to be nearly translucent, and these are often colored a soft pink merging with a light yellowish green. However, pinnae in most mature plants are opaque, deep olive- or gray-green adaxially, with the tissue opaque and nearly coriaceous.

***Adiantum obliquum* Willd. Sp. Pl. 5: 429. 1810.**

In wet forests or thickets, sometimes at edges of forests and along river banks, sea level to 800 m.; Alta Verapaz; Huehuetenango; Izabal; Petén. West Indies; Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants terrestrial; rhizome short- to long-creeping, densely provided with lustrous, amber to castaneous scales, these 1-3 mm. long, lanceolate or linear-lanceolate; leaves densely crowded, 30-60 cm. long, 4-10 cm. broad, long-petiolate; petiole 15-40 cm. long, as long or longer than the lamina, wiry or stout, 0.8-2 mm. thick, triquetrous, but often terete at base, lustrous black or atropurpureous, often partly glaucous, furfuraceous, sparsely to amply pubescent, the trichomes often intermixed with a few scales; lamina firm-herbaceous, slightly lustrous on both sides, simply pinnate, with 8-16 pairs of pinnae and a similar apical segment (or rarely the basal pair of pinnae again pinnate); rachis lustrous, castaneous to atropurpureous or blackish, furfuraceous and pubescent like the petiole; pinnae (larger, proximal ones) 2.5-7 cm. long, 0.8-2.5 cm. broad, alternate, glabrous adaxially, sparsely pubescent along the veins abaxially, lanceolate or narrow-deltoid or -rhomboid, acute, inequilateral at base (acroscopically truncate or subauriculate, basiscopically cuneate or deeply excavate), the sterile margins irregularly biserrate and sometimes shallow-crenate, subsessile or very short-stalked, the dark color of the stalk scarcely or not at all passing into the base of the segment; costa often indistinct, but on the abaxial surface commonly discernible nearly to the pinna apex; veins free, distinct, commonly somewhat prominulous adaxially, obliquely spreading from the costa, 2- to 3-forked, the tips terminating in the marginal teeth; sori short, numerous, borne along both margins nearly or quite to pinna apex.

In Guatemala, this simply pinnate species has been collected very rarely with the basal pair of pinnae greatly enlarged and once again pinnate. Such specimens, even in other areas, are found so infrequently, and lacking a geographical pattern, that it seems unwise to assign them even infraspecific status.

Adiantum obliquum is often very difficult to distinguish from *A. petiolatum*. The glaucous undersurface of the latter is not always obvious, especially in dried material, and many specimens are so com-

pletely soriferous as to render useless the character of sterile pinna margins. Pubescence on rachis and pinnae seems to be an additional feature with which to separate the two species in Guatemala, although this may be less consistent elsewhere in the range. In *A. obliquum*, the rachis tends to be rather amply pubescent, and a few minute trichomes also can be found scattered along the veins of segments abaxially, whereas in *A. petiolatum* the rachis is scarcely, if at all, pubescent, and pinnae are glabrous.

***Adiantum patens* Willd. in L. Sp. Pl. 5: 439. 1810.**

In forests, thickets, and open places, often on rocky slopes, 700-1,600 m.; Huehuetenango; Santa Rosa. Mexico; Honduras; El Salvador; Costa Rica; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Plants terrestrial; rhizome small, short-creeping, provided with linear or lanceolate, orange to dark-brown scales, these 2-3 mm. long, the margins entire, and often minutely and irregularly ciliate; leaves approximate to crowded, 25-70 cm. long, 10-30 cm. broad, long-petiolate, forked at the petiole apex; petiole 12-44 cm. long, longer than the lamina, stout or wiry, 0.8-2.5 mm. thick, flattened or angular, lustrous, light brown to castaneous or atropurpureous, glabrous or puberulent, and often sparsely scaly at base; lamina subflabellate to reniform or nearly circular, the 2 primary branches often arching downward, each of them bearing several pinnalike divisions (penultimate segments) on the outer (acroscopic) side; penultimate segments short-stalked, 1-pinnate, oblong, 5-18 cm. long, 2-3.5 cm. broad, with numerous lateral segments and a usually stalked apical one, tissue papyraceous to membranaceous, glabrous, or sparsely and minutely pubescent abaxially; ultimate segments sessile to short-stalked, dimidiate, oblong or oblong-lunate, the acroscopic margin entire, crenate, or broadly serrate; veins free, several-forked; sori mostly reniform or lunate, only a few to each ultimate segment, borne along the acroscopic margin nearly or quite to the apex.

***Adiantum petiolatum* Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 326. 1811. *A. kaulfussii* Kunze. Linnaea 21: 221. 1848.**

In forests, thickets, or wooded ravines, often along banks of streams, sea level to 350 m.; Alta Verapaz; Izabal; Petén; Retalhuleu; San Marcos; Santa Rosa. West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants terrestrial; rhizome short- to long-creeping, densely provided with lustrous, amber to castaneous scales, these 2-4 mm. long, linear-lanceolate to filamentous; leaves approximate to crowded, 20-45 cm. long, 6-10 cm. broad, long-petiolate; petiole 10-22 cm. long, as long as or longer than the lamina, wiry or stout, 0.5-1.8 mm. thick, triquetrous, but usually terete at base, lustrous-black, atropurpureous, or (occasionally) castaneous, sometimes partly glaucous, sparsely pubescent or glabrate, or with a few, scattered, filiform scales; lamina thin- to firm-herbaceous, dark green and dull to somewhat lustrous adaxially, lighter green and commonly dull and somewhat glaucous abaxially, simply pinnate, with 4-10 (-12) pairs of pinnae and a similar apical segment (or

rarely the basal pair of pinnae again pinnate); rachis lustrous, castaneous to atropurpureous or blackish, sparsely filiform-pubescent or glabrate; pinnae (larger, proximal ones) 2.5-6 cm. long, 1-2.5 (3) cm. broad, alternate, glabrous, lanceolate or narrow-deltoid or -rhomboid, acute to obtuse, inequilateral at base (acroscopically truncate or subauriculate, basiscopically cuneate or deeply excavate), sterile margins regularly and finely serrulate, subsessile or very short-stalked, the dark color of the stalk scarcely or not at all passing into the base of the segment; costa often indistinct, but on the abaxial surface commonly discernible nearly to the pinna apex; veins free, distinct, commonly somewhat prominulous adaxially, obliquely spreading from the costa, 2- to 3-forked, the tips terminating in the marginal teeth; sori short, numerous, borne along both margins nearly or quite to pinna apex.

Although this is a simply-pinnate fern, a few specimens have been collected (outside Guatemala) with the basal pair of pinnae enlarged and once again pinnate. Dried specimens of *A. petiolatum* can be very difficult to distinguish from *A. obliquum* (under which see further discussion).

***Adiantum poiretii* Wikstr.** Kongl. Vetensk. Acad. Handl. 1825: 443. 1826.

In open forests, thickets, and wooded ravines, often on dry, rocky hillsides, 1,700-3,000 m.; Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez; Sololá; Totonicapán. Mexico; El Salvador; Costa Rica; Panama; Colombia and Venezuela, south to Argentina and Chile; Old World tropics.

Plants terrestrial; rhizome short- or long-creeping, provided with castaneous, linear or lanceolate scales, these 2-4 mm. long, the margins entire, or occasionally sparsely and minutely ciliolate, obscurely or not at all clathrate; leaves crowded to subdistant, 24-60 cm. long, 6-14 cm. broad, petiolate; petiole 10-28 cm. long, commonly shorter than the lamina, wiry to stout, 0.5-1.8 mm. thick, terete to flattened, or angular, lustrous, castaneous to atropurpureous, glabrous, or sparsely scaly near the base; lamina delicate, membranaceous, glabrous (at least in ours), 2-pinnate to 3-pinnate, lanceolate to ovate or deltoid-ovate; rachis lustrous, glabrous; pinnae long-stalked, widely spaced, commonly 6-10 pairs, glabrous, most of them with 3-5 pairs of pinnules, the basal pinnule commonly the largest and pinnate or more; ultimate segments subflabellate, lunate or obovate, cuneate to truncate or subcordate at base, crenate to lobed or deeply cleft, with sterile portions of the margin subentire to crenulate, stalked, the stalks not dilated nor articulated at apex, castaneous to atropurpureous, the dark color entering the segment, or if not, then blending gradually and irregularly with the lighter color of the veins; veins free, subflabellate, and 2- to 3-forked, the tips each ending in a sinus (where a sinus is present); sori few on each ultimate segment, often solitary on a segment lobe, most of them oblong, oblong-lunate, or subreniform, the sinus of the indusium broad and shallow or nearly lacking.

Although the features of *A. poiretii* are rather constant in Guatemala, several forms and varieties occur in South America in which the segments are pubescent, glandular, or even farinose. It is very similar to (or perhaps conspecific with) *A. aethiopicum* L. of Africa and

Australia and *A. raddianum* Presl (under which see further discussion). The latter is a plant with irregular distribution throughout the neotropics (often cultivated), with mostly suborbicular sori. Sori in *A. poiretii* are, at most, subreniform, with sinuses very broad and shallow, or even lacking.

Adiantum polyphyllum Willd. Sp. Pl. 5: 454. 1810. *A. cardiochlaena* Kunze, Linnaea 17: 569. 1843.

Rare, in forests, on slopes or river banks, sea level to 150 m.; Izabal. Colombia; Venezuela; Trinidad.

Plants terrestrial; rhizome stout, short-creeping, amply provided with lanceolate, acuminate scales, these 1-3 mm. long, ferruginous or castaneous, larger ones sometimes bicolorous, with a thin, black median stripe in the basal portion; leaves crowded, 50-130 cm. long, 30-70 cm. broad, petiolate; petiole 18-55 cm. long, about as long as the lamina, stout, 1.5-5 mm. thick, terete, usually sulcate adaxially, lustrous, atropurpureous, glabrous, often somewhat scurfy and glaucous at the base; lamina mostly 2-pinnate, but 3- to 4-pinnate as to the lower pinnae, deltoid, firm-herbaceous, glabrous, not or rarely glaucous; rachis glabrous, lustrous, atropurpureous; pinnae 7-10 pairs, stalked, most of them pinnate, but at least the basal pair with their basal pinnules again pinnate or 2-pinnate; ultimate segments dimidiate, oblong or triangular-oblong, obtuse or acute, truncate at base acroscopically, scarcely stalked, the acroscopic margin broadly crenate or shallowly lobed, the lobes subentire to denticulate; veins free, 2- to 3-forked; sori 5-9 on each fertile ultimate segment, borne on the acroscopic margin and often around the tip of the segment, commonly 1 to a lobe or crenation, discrete, short, 1-2 mm. long, often as broad as long, squarish, broadly oblong or semicircular (infrequently subreniform) or, at full maturity globose, the sporangia almost completely enveloping the constricted indusium; indusium plane, commonly dark reddish brown, often with a narrow, light-brown margin, joined with the margin proper in a straight or slightly concave line.

This is most closely related to *A. wilesianum*, under which see further discussion.

Adiantum princeps Moore, Gard. Chron. n.s. 4: 197. 1875.

In forests, thickets, and wooded ravines, often on rocky hillsides, 200-2,100 m.; Chimaltenango; Escuintla; Guatemala; Jutiapa; El Quiché; Santa Rosa; Zacapa. Mexico; Honduras; El Salvador to Panama; Colombia.

Plants terrestrial, rhizome erect or ascending, amply provided with orange or light-brown, concolorous scales, these 3-6 mm. long, obscurely or not at all clathrate, linear or lanceolate, the margins setulose; leaves crowded to caespitose, 50-120 cm. long, 25-40 cm. broad, petiolate; petiole 25-60 cm. long, about as long as the lamina, stout, 1-3 mm. thick, terete, lustrous, atropurpureous to blackish, glabrous, but with a few scales scattered near the base; lamina delicate, membranaceous to firm-herbaceous, commonly 3- to 4-pinnate, deltoid, broadest at base; rachis lustrous, glabrous, castaneous to atropurpureous; pinnae stalked, 8-12 pairs, glabrous, the larger (proximal) ones with 8-12 pairs of stalked pinnules; ultimate segments variable, ovate to obovate or

subflabellate, but most of them broadly oblong or trapeziform, often lobed to deeply cleft, with the margins of sterile pinnae subentire, crenulate or (rarely) broadly and obscurely denticulate, clearly articulate at base, long-stalked, the stalks abruptly dilated at the apex and leaving a thin, flat disk where the segment has fallen away, the dark color of the stalk thus sharply terminating before entering the segment; veins free, subflabellate, and 2-3 times forked, the tips ending at the margin; sori commonly 8-16 on each ultimate segment, reniform to (occasionally) oblong, with indusium firm, pale grayish to whitish, usually persistent, joined with the margin proper in a concave to (occasionally) straight line.

This and *A. tenerum* are easily confused. Although the characters used in the key are consistent, they are not always discernible on herbarium specimens. Leaves are often completely fertile, thus the character of sterile segment margins could be of little use. Collectors consistently fail to take rhizomes, thus there may be no rhizome scales to compare, and the few scales adhering to the petiole base are not usually diagnostic. However, there are two other features which, although not reliable in all cases, seem to be effective in separating most Guatemalan specimens. Shape of ultimate segments varies somewhat in both species, but in *A. tenerum* the majority of segments seem to be rhomboid or obovate and obviously cuneate at base. Segments of *A. princeps* are predominantly trapeziform or, at least, broadly oblong, i.e., with the acroscopic margin nearly parallel with, and the basiscopic margin nearly perpendicular to, the axis on which the segment is borne. Also, indusia in *A. tenerum* are commonly narrow-oblong, thin-textured, and greatly constricted or withering at maturity, whereas indusia in *A. princeps* are mostly reniform, coarse-textured, and persistent.

Both species are part of a larger complex, including *A. fragile* Sw. of the West Indies, and *A. amplum* Presl and *A. trapezoides* Fée of Mexico, to name a few. *Adiantum fragile* seems to be distinct, on the basis of its much smaller size and extremely short petiole. The other two may be conspecific with *A. princeps*, as specimens so determined seem to differ not at all. However, I have not seen types of the Mexican species and a final taxonomic decision must be left to the monographer.

***Adiantum pulverulentum* L. Sp. Pl. 1096. 1753.**

In wet forests, thickets, and wooded ravines, sea level to 800 m.; Alta Verapaz; Escuintla; Izabal; Petén; Quezaltenango; Retalhuleu; San Marcos. West Indies; Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Plants terrestrial; rhizome short-creeping, provided with linear or lanceolate, castaneous scales, these about 1 mm. long, mostly appressed; leaves crowded to subfas-



FIG. 4. *Adiantum* (decompound species). a-b, *A. concinnum*: a, habit, $\times \frac{1}{2}$; b, base of one pinna with rachis and overlapping pinnules; c, *A. capillus-veneris*, ultimate segment, $\times 3$; d, *A. tenerum*, fertile ultimate segment, $\times 3$; e, *A. terminatum*, sterile ultimate segment, $\times 3$; f, *A. pulverulentum*, fertile ultimate segment, $\times 3$.

ciculate, 60-110 cm. long, 20-30 cm. broad, long-petiolate; petiole 32-70 cm. long, as long as or longer than the lamina, lustrous, atropurpureous, terete or somewhat flattened at base, becoming quadrangular distally, densely scurfy and scaly, the scales light or dark brown, subappressed, linear or filiform, 1 mm. long or less, most of them ciliate; lamina chartaceous or subcoriaceous, leaf tissue not glaucous, glabrous or a few minute, filiform (sometimes stellate) scales scattered along the veins, ovate or broadly oblong, 2-pinnate, with 5-9 pairs of pinnae and a similar apical segment, this somewhat or scarcely reduced at base; rachis lustrous, this and the costae scaly (and usually scurfy) as on the petiole; pinnae subsessile or short-stalked, gradually tapering to an attenuate apex; pinnules mostly 0.8-1.8 cm. long, obtuse to subacute, dimidiate, lacking a midrib, somewhat reduced at pinna base, greatly reduced toward pinna apex, the acroscopic margin and apex of sterile segments coarsely and irregularly serrate or crenate-serrate, plane; veins free, subflabellate, and 1- to 2-forked, the tips each ending in a marginal serration; sori often borne throughout the pinna, but never on the apical segment, commonly 1 long, continuous sorus along the acroscopic margin (occasionally joined by another short one) and, very rarely, a short one at the segment apex; indusium relatively thin, erose, subsistent.

Adiantum raddianum Presl, Tent. Pterid. 158. 1836. *A. cuneatum* Langsd. & Fisch. Icon. Fil. 23. 1810 (not Forst. 1786).

Apparently thus far represented in Guatemala by a single collection: on moist bank, area of mixed forest and clearings, hills about 10 km. south of Cobán, Alta Verapaz, 1,400-1,500 m. (*L. O. Williams et al. 40091*). Scattered sparsely throughout Central America and the West Indies, probably often escaped from cultivation; South America.

Plants terrestrial; rhizome short-creeping, provided with castaneous, linear or lanceolate scales, these 2-4 mm. long, the margins entire, obscurely or not at all clathrate; leaves crowded, often subcaespitose, 16-60 cm. long, 6-18 cm. broad, petiolate; petiole 8-30 cm. long, about as long as the lamina, 0.8-2 mm. thick, terete to flattened, or angular, lustrous, castaneous, atropurpureous or blackish, glabrous, or sparsely scaly near the base; lamina delicate, membranaceous, glabrous, (2-) 3- to 4-pinnate, lanceolate to ovate or deltoid-ovate; rachis lustrous, glabrous, castaneous or atropurpureous; pinnae stalked, 6-10 pairs, widely spaced, the basal pair commonly the largest, with 3-7 pairs of pinnules, the basal pinnule the largest and pinnate or more; ultimate segments typically cuneate and subflabellate, usually (but not always) symmetrical, the distal margin shallowly lobed to deeply incised, with sterile margins acutely or subacutely dentate, stalked, the stalks not dilated or articulated at apex, medium brown to atropurpureous, the dark color commonly entering the segment, or if not, then gradually and irregularly blending with the lighter color of the veins; veins free, subflabellate, and 2- to 3-forked, the tips each ending in a well-developed sinus; sori few on each ultimate segment, often solitary on a segment lobe, commonly orbicular-reniform, the sinus of the indusium very narrow, often deep.

The characters separating this and *A. poiretii* are few and mostly inconstant, and the two species are maintained here with great reservations. These, with other species having small, stalked, nonarticulate ultimate segments, are greatly in need of revision, and a clear-cut taxonomy of the complex must wait until then. The character of soral

shape, used in the key, appears to be the only really reliable feature found throughout the total range of the two species—which seems scarcely enough to maintain them at the species level.

***Adiantum seemannii* Hook. Sp. Fil. 2: 5, t. 81a. 1851.**

In forests or thickets, often on steep slopes and along banks of streams, 35-400 m.; Alta Verapaz; Izabal; Petén; Retalhuleu; Suchitupéquez. Mexico (Chiapas); Honduras; Nicaragua; Costa Rica; Panama; Colombia (Chocó).

Plants terrestrial; rhizome short-creeping, amply provided with linear or linear-lanceolate, amber to dark-brown scales, these 1-2 mm. long, rather rigid, the margins entire; leaves approximate to crowded, 30-60 cm. long, 10-22 cm. broad, long-petiolate; petiole 12-36 cm. long, commonly as long or longer than the lamina, rather stout, 1-2.5 mm. thick, terete to flattened or angular, atropurpureous, lustrous, sometimes slightly glaucous, essentially glabrous, but sometimes with a few scattered scales near the base; lamina glabrous, commonly glaucous beneath, firm-herbaceous to chartaceous, simply pinnate, or occasionally (outside Guatemala) the basal pair of pinnae again pinnate, with 2-5 pairs of pinnae and a similar, stalked apical segment; rachis lustrous, atropurpureous, glabrous; pinnae 5-15 cm. long, 1.5-8 cm. broad, alternate, ovate-acuminate, rounded, truncate or broadly cuneate and often inequilateral at base, the sterile margins sharply, deeply, and irregularly serrate, long-stalked (1-4 cm.), the stalks lustrous and atropurpureous, not dilated or cleanly articulated at the pinna base, the dark color not passing into the base of the segment, costa lacking, or indistinct and discernible only in the basal half of the segment abaxially; veins free, distinct, often prominulous, several-forked, extending to the serrate margin, the tips terminating in or between the serrations; sori several or numerous, extending in a scarcely interrupted line along each margin, often nearly to the tip, but ending well short of the base.

Some authors have combined this with *A. platyphyllum* Sw. of Peru and Ecuador. However, specimens of the latter I have seen differ in at least two features. Margins of sterile pinnae are entire to crenulate or broadly and shallowly crenate, and the dark color of the stalk extends well onto the midrib. In *A. seemannii* the sterile margins are deeply and sharply serrate, and the dark color of the stalk does not enter the base of the segment.

***Adiantum tenerum* Sw. Nov. Gen. Sp. Pl. Prodr. 135. 1788.**

In forests and thickets, commonly in crevices of limestone cliffs or rocky slopes, sea level to 1,200 m.; Alta Verapaz; Izabal; Petén. Florida; West Indies; Mexico; British Honduras; Honduras; Costa Rica; Venezuela.

Plants terrestrial or epipetric; rhizome erect, ascending, or very short-creeping, amply provided with castaneous to blackish, commonly bicolorous, scales, these 0.5-2 mm. long, obscurely or not at all clathrate, ovate to linear-lanceolate, the margins ciliate or ciliolate and light brown to scarious at the very edge, the scales at the petiole base sometimes concolorous, often longer and narrower, with marginal cilia frequently de-

ciduous; leaves crowded to subcaespitose, 35-90 cm. long, 18-35 cm. broad, petiolate; petiole 16-48 cm. long, nearly equaling the lamina, wiry, 0.7-2 mm. thick, terete, lustrous, atropurpureous to blackish, glabrous, but with a few scattered scales toward the base; lamina delicate, membranaceous to firm-herbaceous, commonly 3- to 4-pinnate, deltoid, broadest at the base; rachis lustrous, glabrous, castaneous to atropurpureous; pinnae stalked, 7-10 pairs, glabrous, the larger (proximal) ones with 5-7 pairs of stalked pinnules; ultimate segments variable, ovate, obovate, rhomboid, or subflabellate, cuneate, often shallowly to deeply cleft, with the margins of sterile pinnae sharply and conspicuously dentate or denticulate, clearly articulate at base, long-stalked, the stalks abruptly dilated at the apex and leaving a thin, flat disk where the segment has fallen away, the dark color of the stalk thus sharply terminating before entering the segment; veins free, subflabellate, and 2-3 times forked, the tips ending in the marginal teeth; sori 5-12 on each ultimate segment, narrow-oblong to squarish or (rarely) subreniform, with indusium firm and persistent to (most commonly) thin and soon withering, joined with the margin proper in a straight or convex (rarely concave) line.

This often is confused with *A. princeps*, under which see further discussion.

***Adiantum terminatum* Miq. Het. Inst. Versl. Meded. Ned. Inst. Wet. 1842: 3. 1843.**

In forests, near sea level; Izabal (rare). British Honduras; Nicaragua; Trinidad; Guianas to Colombia, south to Bolivia and Brazil.

Plants terrestrial; rhizome slender, short-creeping, amply provided with lanceolate scales, these about 1 mm. long, castaneous to blackish (but to 2 mm. and light brown around the petiole base); leaves approximately to densely crowded, 20-55 cm. long, 18-32 cm. broad, petiolate; petiole 12-30 cm. long, equaling or longer than the lamina, lustrous, castaneous to atropurpureous, commonly quadrangular, amply to abundantly scaly and scurfy; lamina 2-pinnate, with 2-6 pairs of pinnae and a similar apical segment, this rather strongly reduced at base, leaf tissue thin- to firm-herbaceous, abaxially green to slightly glaucous and amply provided with lustrous, castaneous, spreading trichomes to 1 mm. long; rachis and costae scurfy and scaly, the scales light to medium brown, not or slightly lustrous, mostly appressed, filiform, 0.5-1.5 mm. long, with margins entire or (occasionally) minutely and sparsely setulose; pinnae sessile or subsessile, gradually tapering to a lanceolate, occasionally subcaudate, apical segment; pinnules (larger ones of lateral pinnae) 1-2 cm. long, sessile or subsessile, dimidiate at base (truncate acroscopically, sharply cuneate or excavate basiscopically), subequilateral distally, with an indistinct, often barely perceptible midrib running partly to the obtuse (usually broadly rounded, rarely subacute) apex, sterile ones coarsely, but regularly, serrate, those nearest the apical segment greatly reduced ($\frac{1}{4}$ - $\frac{1}{2}$ the length of the larger, central ones); veins free, 1- or 2-forked, diverging from the midrib at a very narrow angle, the tips each terminating in a marginal serration; sori short, discrete, commonly borne from base to apex of pinna (although occasionally the apical segment sterile), 4-10 along the acroscopic margin, 2-3 on the basiscopic, and commonly 1-2 on the acroscopic, base (parallel with the costa); indusium usually thin, joined with the margin in a straight or sometimes concave line.

This scarcely differs from *A. humile* Kunze of South America and *A. killipii* Max. and Weath. of Panama. The latter two were combined by

Tryon (1964), though he maintained *A. terminatum* distinct from both, based on its more numerous sori, its more glaucous lamina, and the more strongly reduced apical pinnules. These characters appear to vary widely, especially in specimens examined from Guatemala and adjacent countries, and a thorough revision of the complex perhaps will show that all three taxa should be combined.

Among the bipinnate species of *Adiantum* with sessile to subsessile leaves, *A. terminatum* may be distinguished by its conspicuously pilose segments. A number of species in this complex are known to bear indument on the abaxial surface of pinnules. But this consists of what appears to be a scattering of minute, simple hairs, mostly confined to the veins near the pinnule base. Each of these processes, as seen under proper magnification, is actually a single line of 2-5 cells broadening gradually or abruptly into a base 2-3 cells wide, which also is frequently stellate. These may be dark-colored—but are more commonly pale—and spreading, and usually are subappressed. Pinnules, abaxially, on *A. terminatum* are amply provided throughout with spreading, lustrous, castaneous trichomes, these uniseriate and narrow to the base.

Adiantum tetraphyllum H. & B. ex Willd. in L. Sp. Pl. 5: 441. 1810.
A. fruticosum Poeppig ex Spreng. in L. Syst. Veg. 4: 113. 1827.

In forests, thickets, and wooded ravines, often on slopes or steep banks, sea level to 1,500 m.; Alta Verapaz; Izabal; Petén; Quezaltenango; Retalhuleu; San Marcos; Santa Rosa; Suchitepéquez. West Indies; Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Plants terrestrial; rhizome short- or long-creeping; amply provided with ovate or lanceolate scales, these usually less than 1 mm. long, castaneous to blackish; leaves crowded to approximate (or occasionally subdistant), 50-100 cm. long, 18-45 cm. broad, long-petiolate; petiole 32-60 cm. long, usually longer than the lamina, lustrous, castaneous to atropurpureous, terete (near the base) or quadrangular, amply scaly and scurfy; lamina 2-pinnate, with 2-6 (8) pairs of pinnae and a similar apical segment, this somewhat (not strongly) reduced at base, leaf tissue firm-herbaceous to chartaceous, green and glabrous or (occasionally) with a few scattered, minute, hairlike scales along the veins abaxially; rachis and costae scaly, the scales tan to medium brown, not or slightly lustrous, mostly appressed, filiform, 0.5-1.5 mm. long, with margins entire to (more commonly) setulose; pinnae subsessile, tapering gradually to an acuminate or attenuate apex; pinnules (larger ones of lateral pinnae) 1-3 cm. long, sessile or subsessile, dimidiate (truncate acroscopically, sharply cuneate, or excavate basiscopically), midrib lacking, or present and barely perceptible toward the subacute or acuminate apex, pinnules at pinna base somewhat reduced, those near the apex gradually and strongly reduced, sterile ones coarsely and irregularly crenate-serrate; veins free, subflabellate, and 2- to 3-

forked, the tips terminating at the margin; sori borne throughout most of the pinna (but never on the apical segment), 4-7 along the acroscopic margin and often 1-2 around the apex; indusium joined with the margin in a straight or somewhat concave line.

There has always been confusion between *A. tetraphyllum* and *A. fructuosum*. Hooker & Baker (Syn. Fil. 120. 1867) combined the two, as has Proctor (1977). Tryon (1964) held them separate "with some hesitation." This is a common fern, widely distributed throughout the American tropics, and the size and shape of the leaf and its segments vary greatly, probably depending on the habitat of individual plants.

Another species with which *A. tetraphyllum* has been confused is *A. villosum*, under which see further discussion.

***Adiantum trapeziforme* L. Sp. Pl. 1097. 1753.**

In forests, thickets, and wooded ravines, often on hillsides or banks of streams, 100-1,800 m.; Alta Verapaz; Escuintla; Huehuetenango; Izabal; Petén; Retalhuleu; Santa Rosa; Zacapa. Mexico to Panama; Cuba; Jamaica; Dominica; Martinique.

Plants terrestrial; rhizome stout, woody, creeping, amply covered with lanceolate to ovate scales, these 1-2 mm. long, castaneous, occasionally with a blackish center, scarcely or not at all clathrate; leaves approximate to well spaced, 50-90 cm. long, 18-38 cm. broad, long-petiolate; petiole 30-55 cm. long, commonly as long as or longer than the lamina, stout, 1.5-3.5 mm. thick, terete (or shallow-sulcate adaxially), lustrous, atropurpureous to blackish, glabrous, but with scales at the base similar to (though larger than) those on the rhizome; lamina glabrous, firm-herbaceous to chartaceous, deltoid-ovate, commonly with 2-4 pairs of stalked pinnae and a similar terminal segment, typically 2-pinnate, but often 3-pinnate as to the basal pinnae; rachis lustrous, atropurpureous to blackish, glabrous; ultimate segments 2.5-5.5 cm. long, mostly dimidiate, trapeziform, lacking a midrib, irregularly serrate or biserrate, crenate, or shallowly to deeply cleft along the distal margins, but the proximal margins entire, the basiscopie one often perpendicular to the costa, the acroscopic one parallel with, or frequently overlapping, the costa, obviously stalked, the stalks glabrous, atropurpureous or blackish, the dark color not entering the segment; veins free, subflabellate, and several times forked, the tips ending in the marginal teeth; sori short, numerous, commonly borne along both the distal margins, semicircular to oblong or subreniform; indusia brown, firm, persistent, joined with the margin in a straight to (rarely) concave line.

This may be confused in Guatemala with the rather rare *A. caryotideum*, under which see further discussion.

***Adiantum tricholepis* Fée, Mém. Fam. Foug. 8: 72. 1857.**

In open forests and thickets, often on rocky hills, 50-200 m.; Petén. Mexico; southwestern United States.

Plants terrestrial; rhizome erect or ascending, provided with orange to castaneous, lanceolate or linear-lanceolate scales, these 2-5 mm. long, short-attenuate, commonly ciliate, obscurely or not at all clathrate; leaves subcaespitose, 30-90 cm. long, 8-30 cm.

broad, petiolate; petiole 15-35 cm. long, equaling or shorter than the lamina, stout or wiry, 0.7-2.5 mm. thick, terete, lustrous, castaneous to atropurpureous, glabrous, sometimes slightly glaucous near the base; lamina delicate, membranaceous to firm-herbaceous, commonly 3- to 4-pinnate, ovate or deltoid-ovate; rachis lustrous, glabrous, castaneous to atropurpureous; pinnae stalked, widely spaced, 6-12 pairs, the minor axes sparsely dark-pilose or glabrate; ultimate segments 0.4-1 cm. long, amply white-pilose (especially abaxially), rhomboid to flabellate or circular, entire to broadly and obscurely crenate or lobed, stalked, the stalks not or scarcely dilated at apex, castaneous to atropurpureous, the dark color terminating abruptly at the base of the segment; veins free, subflabellate, 2- to 3-forked; sori few on each segment, oblong, oblong-lunate, or broadly reniform, the indusium commonly whitish, firm, pilose.

***Adiantum villosum* L. Syst. Nat. ed. 10, 2: 1328. 1759.**

In forests, thickets, and wooded ravines, often in rocky soil, sea level to 1,200 m.; Alta Verapaz; Escuintla; Izabal; Petén; Retalhuleu; Santa Rosa; Suchitepéquez. West Indies; Mexico to Colombia and Venezuela; Peru; Brazil.

Plants terrestrial; rhizome short-creeping, amply provided with ovate to lanceolate scales, these about 1 mm. long, castaneous to blackish, obscurely clathrate; leaves densely crowded on the rhizome, 50-100 cm. long, 18-35 cm. broad, petiolate; petiole 20-60 cm. long, equaling or longer than the lamina, lustrous, atropurpureous or blackish, commonly quadrangular, amply to densely scurfy and scaly; lamina 2-pinnate, with 2-5 pairs of pinnae and a similar apical segment, this scarcely or not at all reduced at base, leaf tissue firm-herbaceous to chartaceous, rarely (if ever) glaucous, adaxially glabrous, abaxially with a few scattered, minute, hairlike scales along the veins of pinnules (especially toward their base), appearing to be simple trichomes, but most of them more than 1 cell broad at the often-stellate base; rachis and costae scaly and often scurfy, the scales tan to medium brown, not or scarcely lustrous, mostly appressed, filiform, 1-1.5 (2) mm. long, their margins often sparsely setulose; pinnae short-stalked to sessile, terminating rather abruptly in an ovate or lanceolate apical segment; pinnules (larger ones of lateral pinnae) 2.2-4 mm. long, sessile or subsessile, dimidiate at base (truncate acroscopically, sharply cuneate, or excavate basiscopically), subequilateral distally, with a definite, often indistinct, midrib running most of the way to the acute or subacute apex, sterile ones coarsely and irregularly serrate or crenate-serrate, those nearest the apical segment not greatly reduced, the ultimate pair usually about $\frac{1}{2}$ the size of the larger, central ones; veins free, 1- or 2-forked, diverging from the midrib at a very narrow angle, the tips each terminating in a marginal serration; sori borne from base to apex of pinnae (although the apical segment occasionally sterile), variable, a single, long, continuous one along the acroscopic margin of each pinnule, or 2-6 discrete or contiguous ones along the acroscopic margin and 1-2 near the apex basiscopically; indusium relatively coarse, joined with the margin proper in a straight to concave line.

This and *A. tetraphyllum* are rather similar, and highly variable, ferns. Of the characters used in the key, that of reduced apical pinnae seems to be the most efficacious. Pinnae of *A. tetraphyllum* are gradually tapered to a narrow, often attenuate apex, with the last 2-3 pairs of segments commonly very minute. In *A. villosum* the pinnae are more abruptly reduced, terminating in a broader, ovate to lanceolate,

apical segment, and the pair of segments next to it are reduced, but rarely less than half the length of the larger, central ones. In addition to the key characters the two species also differ in the nature of the base of the pinnalike apical section of the lamina. In *A. tetraphyllum* this is obviously, though not too greatly, reduced, with the basal pair of segments perhaps half the size of the larger, median ones. In *A. villosum*, however, the apical section is scarcely, if at all, reduced at base.

***Adiantum wilesianum* Hook. Sp. Fil. 2: 50. 1851.**

In forests, commonly on rocky (limestone) slopes, sea level to 400 m.; Alta Verapaz; Izabal; Petén. Mexico; British Honduras; Honduras; Jamaica.

Plants terrestrial; rhizome short-creeping, scaly, the scales 1-2 mm. long, lanceolate or linear-lanceolate, light brown or castaneous; leaves crowded, 50-100 cm. long, 30-48 cm. broad, petiolate; petiole 30-55 cm. long, about as long as the lamina, stout, 1-4 mm. thick, terete to flattened, lustrous, atropurpureous, essentially glabrous, somewhat glaucous; lamina mostly 2-pinnate, but 3- to 4-pinnate as to the lower pinnae, deltoid or subpentagonal, firm-herbaceous, not or scarcely glaucous; rachis lustrous, atropurpureous or blackish, glabrous adaxially, but densely covered abaxially with minute, rigid, simple trichomes, these rarely over 0.1 mm. long; pinnae 4-8 pairs, stalked, most of them simply pinnate, but at least the basal pair with their basal pinnules again pinnate or even 2-pinnate; ultimate segments dimidiate, oblong to oblong-lanceolate, obtuse to acute, or the larger ones often subfalcate and attenuate, truncate at base acroscopically, scarcely stalked, the acroscopic margin broadly crenate or shallowly lobed, the lobes subentire to obscurely denticulate; veins free, 2- to 3-forked; sori 4-6 on each fertile segment, borne on the acroscopic margin, commonly 1 to a lobe or crenation, discrete, 2-3 mm. long, mostly longer than broad, oblong or allantoid, or, at full maturity, ovoid, the sporangia spreading over and almost completely obscuring the constricted indusium; indusium thick-textured, convexly enveloping the developing sporangia, mostly allantoid, dark brown, joined with the margin proper in a straight to (more commonly) concave line.

This and *A. polyphyllum* are closely related, the chief differences being the presence or lack of axial pubescence and shape and character of sorus and indusium, as noted in the key. Two other similar species are *A. brasiliense* Raddi, which has rather long, tortuous, pluricellular trichomes along the axes, and *A. pyramidale* (L.) Willd., an Antillean species with smaller, less dissected, subcoriaceous laminae. (The latter has been more commonly known as *A. crenatum* Willd. or *A. cristatum* L., but Proctor (1977) has shown *A. pyramidale* to be the correct name.

***Adiantum wilsonii* Hook. Sp. Fil. 2: 6, t. 72a. 1851.**

In forests, often near lake shores or stream banks, 80-350 m.; Alta Verapaz; Petén. Mexico (Chiapas); British Honduras; Nicaragua; Costa Rica; Panama.

Plants terrestrial; rhizome long-creeping, amply provided with linear or lanceolate, amber to castaneous, clathrate scales, these to 1 mm. long, appressed, with margins erose and ciliate; leaves several to many, approximate, 20-50 cm. long, 10-18 cm. broad, long-petiolate; petiole 12-40 cm. long, much longer than the lamina, stout, 1-3 mm. thick, terete to flattened or angular, this and the rachis atropurpureous, lustrous, sparsely to amply pubescent, the trichomes appressed, often with a few, scattered, filamentous scales intermixed; lamina chartaceous to subcoriaceous, simply pinnate, with 1-2 (3) pairs of pinnae, and a similar, stalked apical segment; pinnae commonly short-stalked (to 5 mm.) alternate, 6-12 cm. long, 2-4.5 cm. broad, narrowly to broadly ovate, subfalcate, acuminate at the apex, rounded, truncate or cordate at the often-inequilateral base, fertile margins entire, sterile ones irregularly serrate, dark green and glabrous adaxially, lighter green abaxially and often with scattered, minute trichomes near the costa; costa distinct nearly throughout, the dark color of the stalk continuing well into the pinna base; veins indistinct or obscure, several-forked, approximate, springing from the costa at a narrow angle, several to many of them anastomosing to form elongated areoles; sori continuous along both margins, or essentially so, running nearly from base to apex.

This is very similar to *A. dolosum* Kunze of Brazil and the Guianas; indeed, some authors have combined the two. *Adiantum dolosum* consistently has more (3-7 pairs) and narrower pinnae, and nearly all the veins anastomose, so that pinnae are fully (not just partially) areolate. These differences, coupled with the disjunction in range, seem sufficient to warrant the recognition of two distinct species.

ANANTHACORUS Underwood & Maxon

REFERENCE: W. R. Maxon, A new genus allied to *Vittaria*, Contr. U.S. Natl. Herb. 10: 486-487. 1908.

Plants small, epiphytic (rarely reported on wet rocks); rhizome small, short-creeping, amply provided with linear or lanceolate scales, these 3-5 mm. long, grayish brown to castaneous (rarely blackish), iridescent, 4-7 cells (lumina) broad, attenuate, the tip often composed of a short, single longitudinal rib; leaves essentially monomorphic, erect to arching or pendent, approximate to crowded, 12-40 cm. long, 0.4-1.8 cm. broad, simple, linear or linear-lanceolate, entire, sessile; lamina opaque, glabrous, coriaceous, margins plane to somewhat revolute, the costa distinct from lamina base to apex, immersed adaxially, prominent abaxially; venation areolate, the veins obscure, forming 3-5 series of areoles on each side of the costa, lacking included veinlets; sporangia long-stalked, slightly immersed in long, sometimes interrupted, submarginal lines, one each on either side of the costa; indusium lacking; paraphyses numerous, castaneous, spatulate; spores monolete, bilateral, with very thin perine.

Ananthacorus is a monotypic American genus doubtfully distinct from *Vittaria*. It is separated from the latter on the basis of the several (vs. 1) series of areoles on each side of the costa—and little else.

Ananthacorus angustifolius (Sw.) Underw. & Maxon, Contr. U.S. Natl. Herb. 10: 487. 1908. *Pteris angustifolia* Sw. Prodr. 129. 1788. *Vittaria angustifolia* (Sw.) Baker, in Mart. Fl. Brasil 1 (2): 544. 1870.

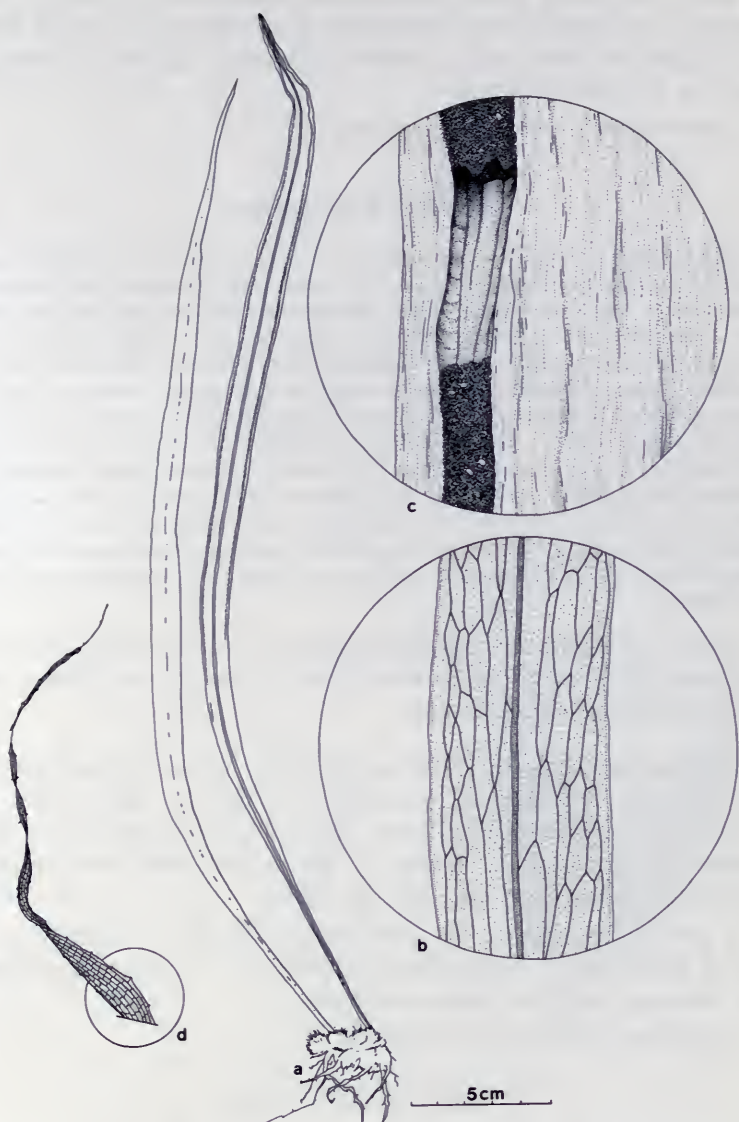


FIG. 5. *Ananthacorus angustifolius*. a, habit, $\times \frac{1}{2}$; b, portion of lamina, adaxial side, $\times 3$; c, margin of fertile lamina with soral line (some sporangia removed to show deep groove), $\times 12$; d, rhizome scale, $\times 12$.

In wet forests, on trunks or branches of trees, very rarely reported on wet rocks along rivers or waterfalls, sea level to 1,200 m.; Alta Verapaz; Chimaltenango; Chiquimula; Huehuetenango; Izabal; Petén; Suchitepéquez. West Indies; Mexico to Panama; Colombia to Surinam, south to Bolivia and Brazil.

Characters are those of the genus.

ANETIUM Splitgerber

Plants small to medium-sized, epiphytic, erect or, more commonly, pendent; rhizome slender, long-creeping, amply provided with dark-brown, iridescent, clathrate scales, these 4-5 mm. long, linear or lanceolate, attenuate, the tip often composed of a single, short, longitudinal rib; leaves monomorphic, approximate to widely spaced, 6-60 cm. long, 2-8 cm. broad, simple, broadly elliptic or (more commonly) oblanceolate, entire, sessile or subsessile; lamina glabrous, or somewhat scaly at the constricted base, drying papyraceous to firm-herbaceous, margins plane or scarcely revolute, sometimes undulate, costa commonly distinct only in the proximal half, plane adaxially, slightly prominulous abaxially; venation indistinct or obscure, copiously areolate, without free, included veinlets, the veins forming many series of pentagonal or hexagonal areoles between margin and costa, finally terminating in free tips near the margin; sporangia stalked, borne singly or in small clusters, sparsely scattered along the veins and sometimes between the veins, abaxially; indusium and paraphyses lacking; spores trilete, tetrahedral.

Anetium is a monotypic, American genus closely allied to *Hecistopteris* and *Polytaenium*. It is an epiphyte of dense, wet forests, commonly growing at low altitudes.

Anetium citrifolium (L.) Splitg. Tijdschr. Natuurl. Gesch. Physiol. 7: 395. 1840. *Acrostichum citrifolium* L. Sp. Pl. 1067. 1753. *Anthrophyum citrifolium* (L.) Fée, Mém. Fam. Foug. 4: 51. 1851. *Hemionitis citrifolia* (L.) Hook. Sp. Fil. 5: 193. 1864. *Pteridanetium citrifolium* (L.) Copel. Gen. Fil. 224. 1947.

In dense, wet forests, on tree trunks, 35-200 m., Alta Verapaz; Izabal; Petén. West Indies; British Honduras to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Characters are those of the genus.

ANOGRAMMA Link

REFERENCES: K. Domin, Generis *Pityrogramma* (Link) species ac sectiones in clavem analyticam dispositae, Spisy Prir. Fak. Karlový Univ. 88: 1-10. 1928. R. Tryon, The genus *Anogramma*, in: Taxonomic fern notes II, Contr. Gray Herb. 189: 74-76. 1962.



FIG. 6. *Anetium citrifolium*. a, habit, $\times \frac{1}{2}$; b, portion of lamina, adaxial surface, showing costa and veins, $\times 3$; c, abaxial surface, showing sporangia scattered irregularly along and between veins, $\times 6$; d, rhizome scale, $\times 12$.

Plants annual (at least the sporophyte), terrestrial, delicate; rhizome small, erect, sparsely scaly or with a few septate trichomes; leaves monomorphic (or essentially so), erect, fasciculate, to 30 cm. long; petiole not articulate, delicate, smooth, lustrous, light brown to castaneous, darkest at base, essentially glabrous, but sometimes with a few, scattered, minute septate trichomes or filamentous scales; lamina commonly decompound, often shorter than the petiole, glabrous, thin- to firm-membranaceous, gradually tapering to a pinnatifid apex; pinnae commonly less than 10 pairs, most of them stalked, spreading to ascending; ultimate segments small, obovate to linear; veins free, simple, or 1-forked in the ultimate segments; sporangia borne abaxially along the veins, sometimes confluent and then nearly covering the segment at maturity; paraphyses and indusia none; spores trilete, tetrahedral, with perine.

Anogramma is a small genus of six or seven ill-defined species, chiefly confined to tropic or subtropic regions in the New World, but with one species nearly cosmopolitan. The sporophyte is annual, with delicate, usually small leaves, hence it is not a very conspicuous part of the vegetation, and can be easily overlooked by collectors. Most of its species are distinguished by little more than size and shape of lamina and segments, but more careful field observations will be required to substantiate true relationships. Only one species has been reported from Guatemala.

Anogramma guatemalensis (Domin) C. Chr. Index Fil. Suppl. III: 26. 1934. (Type from "Fuego," *Salvin & Godman 172*, probably Volcán Fuego, situated on the border between Chimaltenango and Sacatepéquez.) *Pityrogramma guatemalensis* Domin, Spisy Prir. Fak. Karlový Univ. 88: 5. 1928.

In wet forests or shaded ravines, often along stream banks, 1,600-2,850 m., Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; Sacatepéquez. Mexico, Costa Rica, and probably in scattered locations in between.

Rhizome small to rudimentary, provided with a few, minute, castaneous, septate trichomes or with several filamentous scales; leaves several, crowded or fasciculate, 6-25 cm. long, 2-5 cm. broad; petiole 4-12 cm. long, commonly less than 1 mm. thick, nearly equaling to somewhat longer than the lamina, glabrous except for a few basal, septate trichomes, these 1 mm. long or less; lamina linear to ovate, glabrous, membranaceous, 3- to 4-pinnate, not or scarcely reduced at base; rachis glabrous, castaneous to (distally) stramineous, lustrous; pinnae subdistant, stalked, ascending or (rarely) spreading; the pinnules anadromous, stalked, pinnate to nearly 2-pinnate; ultimate segments linear-spathulate, 1-3 mm. long, commonly less than 1 mm. broad, obtuse, often retuse or sometimes bifid; veins commonly simple in the segments, or occasionally forked (in bifid segments), terminating short of the segment apex.

Tryon (1962) suggested that *A. guatemalensis* may be a variant of the cosmopolitan *A. leptophylla* (L.) Link. Gastony and Baroutsis have



FIG. 7. *Anogramma guatemalensis*. a, habit, $\times \frac{1}{2}$; b, pinna (adaxial surface), $\times 13$; c, pinna (abaxial surface) and sporangia, $\times 13$.

been undertaking cytological work on the genus, and in some of their studies (*e.g.*, Amer. Fern J. 65: 71-75. 1975) they seem, thus far, to be of the same opinion. Morphologically, *A. guatemalensis* appears to differ from *A. leptophylla* only in its somewhat more dissected lamina and relatively narrower segments. In some areas the two species have been collected together, with evidence of some transitional states.

ANTROPHYUM Kaulfuss

REFERENCES: R. C. Benedict, The genus *Antrophyum*, Bull. Torrey Bot. Club 34: 445-458. 1907; and, The genera of the fern tribe Vittarieae, *op. cit.* 38: 153-190. 1911. R. M. Tryon, Taxonomic fern notes, IV: Some American vittarioid ferns, Rhodora 66: 110-117. 1964.

Plants small to medium-sized, epiphytic (in ours) or epipetric; rhizome rather thick, short-creeping to ascending, clathrate-scaly, and clothed with masses of golden-tomentose roots; leaves monomorphous, not articulate, simple and entire, crowded to subfasciculate, to 70 cm. long and 12 cm. broad, commonly (as in ours) very narrow, but in a few species to 18 cm. broad and the lamina sometimes as broad as long; petiole commonly short or essentially lacking; lamina glabrous, fleshy when living, firm-herbaceous to chartaceous when dried, with costa essentially lacking, or evident in only the proximal $\frac{1}{4}$ - $\frac{1}{2}$ of the lamina, or (as in ours) sometimes evident toward the apex abaxially, but then plane and broad, never prominulous; venation indistinct or obscure, areolate, the areoles in several series between costa and margin, without free, included veinlets; sporangia stalked, immersed in shallow grooves, or rarely nearly superficial, borne abaxially along the (usually longitudinal) veins, in crooked or forked patterns (rarely fully reticulated); indusium lacking; paraphyses numerous; spores monolete and bilateral (as in ours) or trilete and tetrahedral (mostly in Asian species).

This and *Polytaenium* are closely related, so much so that the two genera are united by some authors (see treatment of the latter for further discussion). *Polytaenium* is a neotropical genus, while *Antrophyum* is comprised of 25-30 paleotropical species, in addition to ours, the lone American representative.

Antrophyum ensiforme Hook. in Benth. Pl. Hartweg. 73. 1841.
Scoliosorus ensiformis Moore, Index Fil. xxix. 1857.

In dense, wet forests, commonly pendent from tree trunks, 1,200-2,800 m., Alta Verapaz; Baja Verapaz; Chimaltenango; Huehuetenango; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Suchitepéquez; Zacapa. Mexico to Panama.

Plants epiphytic; rhizome amply to densely provided with ovate to linear-lanceolate scales, these light brown or grayish brown, somewhat iridescent, 0.5-1.5 cm. long; leaves 10-70 cm. long, 1-3.2 cm. broad, narrowly or broadly oblanceolate, sessile; lamina opaque, glabrous, broadest above the middle, the apex acute, the margins plane or slightly revolute, tapering very gradually to base, lacking a free petiole, costa flush with the surface or very slightly raised, indistinct, commonly seen as a central band of discolored tissue, running $\frac{1}{2}$ - $\frac{3}{4}$ of the way to the apex (or less, as seen from the adaxial side); veins areolate, the areoles in 3-5 series on each side of the costa, very long and narrow along the costa, becoming progressively shorter and broader toward the margin, and ending near the margin in free tips; soral lines slightly immersed; paraphyses yellow-brown to castaneous, with a thin, pedicel-like base, the tip abruptly and conspicuously enlarged; spores monolete, bilateral, elliptic, or subreniform.

Copeland and others have recognized this as a monotypic genus, *Scoliosorus*, on the strength of its monolete, bilateral spores and os-



FIG. 8. *Antrophyum ensiforme*. a, habit, $\times \frac{1}{2}$; b, portion of lamina and margin with sori, $\times 7$; c, rhizome scales, $\times 7$.

tensibly percurrent costa. However, the spores scarcely differ from those of most African species of *Antrophyum*, and the "percurrent costa" in *A. ensiforme* for most of its length is hardly more than a broad band of lighter colored tissue—certainly not the firm, strongly prominulous costa seen on the abaxial side of leaves of *Polytaenium*, the most closely related genus.

ARACHNIODES Blume

REFERENCES: C. Christensen, Subgenus XI *Polystichopsis* (pp. 101-120) in: A monograph of the genus *Dryopteris*, Part II. . . . Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII (6): 1-132. 1920. C. V. Morton, *Byrsopteris*, in: Observations on cultivated ferns VI. . . . Amer. Fern J. 50: 149-154. 1960. M. D. Tindale, Studies in Australian Pteridophytes 3: *Arachniodes*, Contr. New So. Wales Natl. Herb. 3: 89-90. 1961.

Plants terrestrial, erect; rhizome scaly, short-creeping with leaves approximate or subfasciculate (in ours) or long-creeping with leaves subdistant; leaves monomorphous, erect, the axes sparsely (in ours) or amply provided with scales and very rarely with a few isolated, articulate trichomes; petiole not articulate; lamina 3- to 5- (6-) pinnate, essentially eglandular, firm-herbaceous to (in ours) subcoriaceous, broadly deltoid, tapering to a pinnatifid apex, axes with raised ridges adaxially, which are decurrent onto those of the next order below; pinnae greatly dissected, with segments anadromous, the ultimate segments commonly (as in ours) spinulose-serrate; venation anadromous, the veins free, branched, usually reaching the margin; sori abaxial on the vein branches, round or subreniform; indusium circular-reniform, attached at the sinus; paraphyses lacking; sporangia long-stalked; spores monolete, bilateral, with perine.

Arachniodes occupies a phyletic position about halfway between *Dryopteris* and *Polystichum*, possessing a number of the characters of each. The American species of the genus were formerly included by Christensen in his treatment of *Dryopteris*, as part of the subgenus *Polystichopsis*. These were part of a large group of species allied with *Dryopteris aristata* (Forst. f.) O. Ktze., which Morton (1960) assigned to his new genus, *Byrsopteris*. However, as Tindale (1961) pointed out, Morton had overlooked the genus *Arachniodes* Blume (Enum. Pl. Java 241. 1828), which cannot be replaced by *Byrsopteris*.

Arachniodes, as currently recognized, consists of 40-50, predominantly Asian, species. There are four American species, one of which is found in Guatemala.

Arachniodes denticulata (Sw.) Ching, Acta Bot. Sin. 10: 260. 1962. *Polypodium denticulatum* Sw. Prodr. Fl. Ind. Occ. 134. 1788. *Aspidium denticulatum* (Sw.) Sw. J. Bot. (Schrader) 1800 (2): 40. 1801.



FIG. 9. *Arachniodes denticulata*. a, habit, $\times \frac{1}{2}$; b, pinnule apex, $\times 2$; c, configuration of axes, adaxial side, greatly enlarged.

A. jucundum Fée, Mém. Fam. Foug. 10: 41. 1865. *Dryopteris denticulata* (Sw.) O. Ktze. Rev. Gen. Pl. 2: 812. 1891. *Dryopteris formosa* (Fée) Maxon *p.p.*, Contr. U.S. Natl. Herb. 13: 17. 1909. *Rumohra denticulata* (Sw.) Copel. Gen. Fil. 114. 1947. *Byrsopteris denticulata* (Sw.) Morton, Amer. Fern J. 50: 152. 1960.

In wet forests, often on slopes or banks of ravines, commonly terrestrial but occasionally found growing on the bases of large trees, 1,200-3,200 m.; Alta Verapaz; Baja Verapaz; Chiquimula; Huehuetenango; Jalapa; Quezaltenango; El Quiché; San Marcos; Zacapa. Southern Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama; Greater Antilles; Venezuela and Colombia, south to Peru and Brazil.

Rhizome stout, short-creeping, densely scaly, the scales lustrous, light or dark brown, linear to lanceolate, entire, or with a few, remote, minute teeth; leaves approximate or subfasciculate, 20-80 cm. long, 8-25 cm. broad; petiole 10-60 cm. long, commonly equal to or longer than the lamina, drying stramineous or light brown, reddish brown and sparsely scaly toward the base, smooth and often lustrous; lamina 3- to 5- (6-) pinnate, subcoriaceous, lustrous, broadly deltoid or often appearing pentagonal due to the large, basiscopically produced basal pinnae; rachis stramineous, glabrous or sparsely beset with brown, hairlike scales; pinnae 10-20, stalked, ascending, crowded or imbricate, inequilateral at base, the basal pair with basal basiscopic pinnules much larger than the acroscopic ones, but in all other pinnae the basal acroscopic pinnules much the largest; ultimate segments ovate to oblong or obovate to oblanceolate, cuneate at base, deeply incised or serrate, spinulose; veins pinnately branched in the segments, the branches extending into the serrations, terminating short of the margin, the tips somewhat enlarged.

For this species, Christensen (1920) recognized numerous forms and varieties, some of which he failed to name and/or fully describe. Size and texture of lamina and degree of acuteness of segments formed the basis for most of his delimitations. His decisions were often based on scanty collections and no keys were provided for these minor taxa, so the entire question remained rather confused. A reexamination of the species and its variants throughout the range, based on current, more complete material, is advised. It is also likely that the Cuban *Aspidium cubense* Kuhn (= *Dryopteris formosa* (Fée) Maxon, *p.p.*, in Christensen's monograph, pp. 119-120) belongs here, but does not merit specific status.

ASPLENium L.

REFERENCES: W. R. Maxon, *Asplenium trichomanes* and its American allies, Contr. U.S. Natl. Herb. 17: 133-153. 1913. Georg Hieronymus, *Asplenium* species novae et non satis notae, Hedwigia 60: 210-266. 1919; and, Kleine mitteilungen über pteridophyten, *op. cit.*

61: 4-39. 1920. C. V. Morton & D. B. Lellinger, The Polypodiaceae subfamily Asplenoideae in Venezuela, Mem. New York Bot. Gard. 15: 1-49. 1966. A. R. Smith, *Diplazium delitescens* and the neotropical species of *Asplenium* sect. *Hymenasplenium*, Amer. Fern J. 66: 116-120. 1976.

Plants terrestrial, epiphytic, or, less frequently, epipetric; rhizome erect to ascending or (infrequently) creeping, sparsely to abundantly scaly, the scales obviously clathrate (with lumina broad and clear) or sometimes inconspicuously so (with lumina narrow and crowded), with margins usually entire, but rarely appearing toothed or ciliate due to the absence of marginal lumina walls; leaves monomorphic (or dimorphic in *A. trichomanes-dentatum*), short- to long-petiolate, of small to moderate size (ours rarely over 60 cm. long); petiole not articulate, glabrous or scaly (especially at base) or very rarely septate-hairy, terete to somewhat flattened, or adaxially sulcate, occasionally alate; lamina pinnate to 3-pinnate-pinnatifid or rarely simple, essentially glabrous, but in a few species with minute, 1-celled or septate trichomes, membranaceous to subcoriaceous, linear to ovate or subdeltoid, terminating in a conform apical segment, or more commonly tapering to a pinnatifid or serrate apex, the tip not infrequently proliferous; rachis glabrous or sparsely scaly, rarely septate-hairy, occasionally alate; pinnae several to many, spreading to ascending, subequilateral to (more commonly) inequilateral at base, more strongly produced acroscopically than basiscopically (or in *A. pumilum* the converse is true); venation free (or anastomosing in a few species outside Guatemala), the veins simple or branched, ending short of the margin, sometimes provided at apex with enlarged hydathodes, these visible on the adaxial surface; sori elliptic to (more commonly) linear, occasionally confluent at maturity, borne along the acroscopic side of veins or, in several species, a few of them along the basiscopic side (these thus diplazioid, i.e., paired, back-to-back); indusium narrow, often delicate and hyaline, attached along the vein and opening toward the midrib (or on diplazioid sori, opposing indusia opening toward the margin), commonly persistent, though sometimes shriveling at maturity; paraphyses lacking; sporangium glabrous, the stalk relatively long and slender, composed of a single row of cells; spores monolete, bilateral, commonly with a number of sharp folds in the perine.

Asplenium is a large, cosmopolitan genus consisting of over 600 species, the greatest proportion of which are found in tropical or subtropical areas. Some of its species have been confused with those of *Diplazium* and, to a lesser degree, *Athyrium*. Sori of the latter (at least those toward the base of the segment) are reniform or hooked, extending along one side of a vein and then curving across to the other side, while sori of *Asplenium* and *Diplazium* are essentially straight. Sori in *Asplenium* are commonly borne on only one side of the vein, with the indusium opening toward the midrib, whereas in *Diplazium* some of the sori (usually proximal ones) are double, i.e., back-to-back, one on each side of the vein. While this character is diagnostic in most cases, there are a few species of *Asplenium* in which double sori can be found.

Rhizome scales, sporangia, and leaf size are other features useful in separating *Diplazium* from *Asplenium* and *Athyrium*. In the latter,

rhizome scales are usually rather obviously clathrate, with lumina broad and clear, often translucent, and contrasting markedly with their surrounding walls; sporangia stalks are composed of a single row of cells; leaves are quite small or medium-sized, only rarely (at least in Guatemala) exceeding 60 cm. in length. In *Athyrium* and *Diplazium*, rhizome scales are, at best, subclathrate, with the lumina darker in color and contrasting slightly, if at all, with the walls; cells of the sporangia stalks are in two or three rows; leaves in most species of *Diplazium* are large and coarse, commonly well over 1 m. in length; in *Athyrium* they are usually medium-sized.

Alan Smith (University of California, Berkeley) has recently transferred *Diplazium delitescens* Maxon to *Asplenium* (Amer. Fern J. 66: 116-120. 1976). In this excellent paper, a number of other characters are outlined and amply described, which affords a convenient aid in the further delineation of the two genera.

N.B. One of the characters employed in the following key to separate large groups of species is that of color and luster of the petiole. Generally this can be a quick and effective method of delineating certain natural species complexes. A number of species with polished, black petioles are not likely to be confused with those having somewhat succulent, green or a grayish petioles. Unfortunately the key functions less easily in the middle ground described as "dark brown" vs. "reddish or gray-brown," especially when a petiole *may* appear slightly lustrous under strong light and high magnification. In keying out certain of these species, discretion is advised in interpreting the meaning of each phrase in the key, for the combination of *both* color and luster must be used.

- a. Lamina simple, undivided. *A. serratum*.
- a. Lamina pinnate to 3-pinnate.
 - b. Rachis and often costae sparsely to abundantly provided with scales, these obviously clathrate (or filiform with an abruptly broadened, clathrate base).
 - c. Lamina 2-pinnate to 2-pinnate-pinnatifid, commonly with a proliferous apex...
A. commutatum.
 - c. Lamina pinnate to pinnate-pinnatisect, not proliferous.
 - d. Lamina abruptly terminating in a conform or subconform apical segment; pinnae serrate or biserrate, medial ones 7-14 cm. long. *A. serra*.
 - d. Lamina gradually diminishing to a pinnatifid apex; pinnae cut nearly to the costa, not more than 5 cm. long. *A. praemorsum*.
 - b. Rachis and costae with scales lacking or hairlike and inconspicuous.
 - e. Basal pair of pinnae more strongly produced basiscopically than acroscopically; lamina often minutely to conspicuously whitish septate-hirsutulous, especially on veins and margins. *A. pumilum*.
 - e. Basal pair of pinnae cuneate or excavate basiscopically; lamina not septate-hirsutulous.

- f. Petiole and base of rachis highly lustrous and dark brown, atropurpureous or blackish (adaxially green in *A. exiguum*).
- g. Lamina simply pinnate, rarely over 3 cm. broad.
- h. Pinnae deeply biserrate, lacerate, or lobed (at least acroscopically).
- i. Leaves 3-10 cm. long; pinnae 6-14 pairs; petiole bicolorous, bright green adaxially, dark brown abaxially; rachis often proliferous at apex.
A. exiguum.
- i. Leaves 14-40 cm. long; pinnae numerous; petiole atropurpureous or blackish, narrowly green-alate adaxially; rachis not proliferous.
A. formosum.
- h. Pinnae subentire to crenate or broadly and shallowly serrate.
- j. Enlarged hydathodes evident near segment margin (visible on adaxial side).
- k. Rhizome scales commonly blackish and obscurely clathrate, the lumina narrow and the walls thick; petiole atropurpureous, rarely dark brown; pinna "stalk" essentially concolorous, green all the way from the rachis surface. *A. monanthes*.
- k. Rhizome scales commonly brownish and obviously clathrate, the lumina broad and clear and the walls thin; petiole dark brown, rarely atropurpureous; pinna "stalk" often bicolorous, the brown coloration abruptly changing to green just below the pinna base.
A. castaneum.
- j. Enlarged hydathodes absent.
- l. Sori 1 (2) to a pinna; lamina scarcely or not at all reduced toward base. *A. olivaceum*.
- l. Sori commonly 2-4 pairs to a pinna; lamina strongly reduced toward base.
- m. Fertile veins (except basal ones) simple, evident, at least by transmitted light; sori borne nearer the midrib than the margin; alt. 150-1,600 m. *A. heterochroum*.
- m. Fertile veins commonly forked, but often obscured within the opaque tissue; sori mostly crowding the margin; alt. 1,800-3,900 m.
A. resiliens.
- g. Lamina 2-pinnate or more, or if simply pinnate, then 4-10 cm. broad.
- n. Lamina simply pinnate, lacking a proliferous bud or radican apex.
- o. Pinnae deeply lacerate; sori subparallel with the costa. *A. dissectum*.
- o. Pinnae entire to crenate or serrate; sori spreading at wide angles to the costa.
- p. Lamina chartaceous to subcoriaceous, imparipinnate, terminating abruptly in a subconform apical segment; pinnae 5-8 pairs; rhizome erect or ascending. *A. kellermanii*.
- p. Lamina thin-herbaceous, gradually diminishing to a narrow, pinatifid apex; pinnae 10-20 pairs; rhizome short-creeping. *A. laetum*.
- n. Lamina 2-pinnate or more, or if simply pinnate, then with a proliferous bud or radican apex.
- q. Petiole 1-2 (3) cm. long; lamina gradually and strongly reduced at base, the lowermost pinnae commonly 2-3 mm. long. *A. rutaceum*.
- q. Petiole 4-16 cm. long; lamina scarcely reduced at base, the lowermost pinnae of mature leaves rarely less than 3 cm. long [*A. radicans*].

- r. Lamina pinnate to nearly 2-pinnate, the secondary segments (if any) adnate to a broadly alate costa.
 - s. Pinnae broadly serrate, not lobed or auriculate. *A. radicans* var. *cirrhatum*.
 - s. Pinnae lobed to deeply pinnatisect (but never cut entirely to the costa). *A. radicans* var. *radicans*.
- r. Lamina 2-pinnate to 3-pinnate, at least the larger secondary segments definitely stalked.
 - t. Pinnae pinnate (at least in the proximal half), the pinnules coarsely toothed. *A. radicans* var. *partitum*.
 - t. Pinnae pinnate-pinnatifid to 2-pinnate. *A. radicans* var. *uniseriale*.
- f. Petiole and base of rachis not or scarcely lustrous, green, reddish, or gray-brown (rarely dark, and then not highly lustrous).
- u. Lamina 2-pinnate to 3-pinnate (at least as to bases of pinnae) or, if not fully 2-pinnate, then the secondary segments 8-20 pairs, these much longer than broad.
 - v. Lamina conspicuously reduced at base; leaves (at least in ours) to 11 cm. long. *A. myriophyllum*.
 - v. Lamina not or scarcely reduced at base; mature leaves (10) 12-100 cm. long (or 4-9 cm. long in *A. cuspidatum* var. *tenerrimum*).
- w. Pinnae commonly sessile, or if ostensibly stalked then the pinna base narrowly decurrent.
 - x. Pinnae sessile, the basal pinnules overlapping the rachis; secondary segments mostly about as broad as long. *A. cristatum*.
 - x. Pinnae subsessile or ostensibly stalked, the basal pinnules not overlapping the rachis; secondary segments commonly much longer than broad.
 - y. Secondary segments deeply incised, the ultimate segments much longer than broad; indusium linear, 0.1-0.3 mm. broad; rhizome scales linear, mostly 0.1-0.5 mm. broad. *A. solmsii*.
 - y. Secondary segments broadly serrate, or lobed, and then the lobes about as broad as long; indusium elliptic, 0.7-1.2 mm. broad; rhizome scales lanceolate to ovate, mostly 1-3 mm. broad. *A. achilleifolium*.
- w. Pinnae (most of them) stalked, the stalks free.
 - z. Ultimate segments commonly obovate or cuneiform.
 - aa. Lamina 3-pinnate nearly throughout; rhizome scales minute, about 1 mm. long; tissue thin and subtranslucent, the veins distinct. *A. breedlovei*.
 - aa. Lamina 2-pinnate (but 3-pinnate as to the bases of larger pinnae); rhizome scales relatively large, to about 5 mm. long; tissue thick, opaque, the veins immersed and indistinct or obscure. *A. cuneatum*.
 - z. Ultimate segments commonly lanceolate, narrowly ovate, or elliptic [*A. cuspidatum*].
 - bb. Mature leaves 4-9 cm. long; petiole 0.2-0.4 mm. thick; ultimate segments 0.4-0.7 mm. broad. *A. cuspidatum* var. *tenerrimum*.
 - bb. Mature leaves (10) 12-50 cm. long; petiole (0.4) 0.6-2 mm. thick; ultimate segments 0.4-2.2 mm. broad.

- cc. Lower pinnae simply pinnate (at least near the base), the pinnales mostly serrate. *A. cuspidatum* var. *cuspidatum*.
- cc. Lower pinnae pinnate-pinnatifid to nearly 3-pinnate, the pinnales pinnatifid or more.
- dd. Lower pinnae pinnate-pinnatifid to nearly 2-pinnate, the tertiary segments adnate, rarely or never stalked.
A. cuspidatum var. *tripinnatum*.
- dd. Lower pinnae 2-pinnate to nearly 3-pinnate, the tertiary segments commonly stalked.
A. cuspidatum var. *foeniculaceum*.
- u. Lamina simply pinnate, or if nearly 2-pinnate at base then the nearly free pinnules only 1-4 pairs, these 1 (2) times as long as broad.
- ee. Petiole conspicuously alate (especially on the distal half), each of the wings 0.3-2 mm. broad.
- ff. Lamina abruptly terminating in a ligulate tip which bears a proliferous bud; basal pinnae not or scarcely reduced; rhizome scales ovate, commonly 2 mm. long. *A. alatum*.
- ff. Lamina gradually reduced to a pinnatifid or serrate apex, not (or rarely) proliferous; basal pinnae (and several other proximal ones) somewhat reduced; rhizome scales linear to lanceolate, 3-6 mm. long.
- gg. Pinnae with acroscopic margins partly 2-serrate; veins (acroscopic ones) often forked; sori 3-8 mm. long, 1 or 2 proximal ones often double (diplazoid). *A. williamsii*.
- gg. Pinnae with margins simply serrate; veins unbranched; sori 1.5-3 (4) mm. long, never diplazoid. *A. pteropus*.
- ee. Petiole nonalate, or marginate or inconspicuously alate toward the lamina.
- hh. Rhizome creeping (sometimes very short).
- ii. Lamina terminating abruptly in a conform or subconform apical segment. *A. repandulum*.
- ii. Lamina gradually diminishing to a pinnatifid apex or terminating in a nonconform apical segment.
- jj. Pinnae 10-20 pairs; sori rarely diplazoid. *A. laetum*.
- jj. Pinnae 5-8 pairs; sori sometimes diplazoid.
- kk. Leaf 30-50 cm. long, 15-24 cm. broad; pinnae attenuate at apex. *A. delitescens*.
- kk. Leaf 10-20 cm. long, 3.5-6 cm. broad; pinnae obtuse to subacute at apex. *A. hoffmannii*.
- hh. Rhizome erect or ascending.
- ll. Lamina with a distinct, conform or subconform apical segment.
- mm. Pinnae entire or essentially so; sori medial. *A. falcinellum*.
- mm. Pinnae crenate to serrate; sori mostly inframedial.
- nn. Pinnae subequilateral, cuneate at base; pinnae 3-5 pairs; petiole and rachis essentially lacking scales. *A. tuerckheimii*.
- nn. Pinnae (most of them) inequilateral at base; truncate and often auriculate acroscopically, cuneate or excavate basiscopically; pinnae (5) 6-15 pairs; petiole (and often rachis) filiform-scaly. *A. feei*.
- ll. Lamina gradually or abruptly reduced to a pinnatifid, serrate, or nonconform apex.

- oo. Leaves dimorphous, the sterile shorter and often spreading in a basal rosette, the fertile erect and central, 2-3 times longer than the sterile; pinnae rarely more than 12 mm. long.
A. trichomanes-dentatum.
- oo. Leaves not dimorphous; pinnae (middle ones of mature leaves) commonly 1.5-7 cm. long.
- pp. Veins commonly indistinct or obscure; lamina not or scarcely reduced at base.
- qq. Lamina terminating in a broad-based, nonconform apical segment; indusium thin, delicate. *A. abscissum.*
- qq. Lamina terminating in a narrow, serrate-ligulate, or indefinite apex; indusium relatively thick, fleshy.
- rr. Pinnae 2-3 times longer than broad, serrate or crenate-serrate, the serrations mostly broad and rounded.
A. auriculatum.
- rr. Pinnae 4-8 times longer than broad, subentire to pinnatisect (if serrate, the serrations mostly narrow and acute) [*A. auritum*].
- ss. Pinnae mostly obtuse to acute, with margins entire to 2-serrate; basal acroscopic auricle (if any) low, rounded, scarcely incised; alt. 0-900 m.
A. auritum var. *auriculatum.*
- ss. Pinnae mostly acute to caudate, with margins conspicuously biserrate, or crenate, lobed or pinnatifid; basal acroscopic auricle (at least of proximal pinnae) conspicuous, often deeply incised; alt. 70-2,000 m.
- tt. Pinnae bicrenate-serrate, or rarely with a few shallow lobes; acroscopic auricle moderately to deeply incised. *A. auritum* var. *auritum.*
- tt. Pinnae mostly pinnatifid; basal acroscopic segments deeply incised, often nearly free (but not stalked). ...
A. auritum var. *bipinnatifidum.*
- pp. Veins distinct; lamina somewhat to greatly reduced at base.
- uu. Pinnae (most of them) with a nearly free acroscopic auricle.
A. sessilifolium.
- uu. Pinnae not auriculate, or only slightly so, and then the basal lobe only shallowly incised.
- vv. Pinnae commonly attenuate; rhizome scales 5-10 mm. long, attenuate, with filiform, tortuous tips; sori relatively long, inframedial. *A. harpeodes.*
- vv. Pinnae obtuse to subacute; rhizome scales 2-3 mm. long, short-attenuate, but not filiform-tipped; sori relatively short, mostly medial. *A. miradorensis.*

Asplenium abscissum Willd. in L. Sp. Pl. ed. 4, 5: 321. 1810. *A. polymorphum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 56, t. 15, f. 2, 1842 (type from Xalapa, Veracruz, Mexico, *Galeotti* 6295) (not Wall. 1828). *A. firmum* Kze. Bot. Zeit. (Berlin) 3: 283. 1845.

On banks in wet forests, and in shaded ravines, 350-2,500 m.; Alta

Verapaz; Petén; Quezaltenango; Santa Rosa. Florida; West Indies; southern Mexico; British Honduras; El Salvador; Honduras; Nicaragua to Colombia and Venezuela, south to Brazil and Bolivia.

Plants terrestrial; rhizome short, erect or ascending, provided at apex with a tuft of linear or lanceolate, slightly lustrous, rather rigid scales, these 1-2 mm. long, obscurely clathrate, flat or somewhat convex, not attenuate, gray-brown to blackish or often blackish with narrow, brown margins; leaves pinnate, crowded to subcaespitose, mature ones (in ours) 15-37 cm. long and 4-11 cm. broad; petiole rather stout, 5-16 cm. long, equaling or slightly shorter than the lamina, dull gray, or greenish to greenish brown, essentially glabrous, abaxially terete, adaxially marginate or very narrowly green-alate; lamina ovate or oblong, glabrous, thin- to firm-membranaceous, not reduced at base, terminating gradually in a broad-based, nonconform apical segment, not proliferous; rachis glabrous, stramineous to red- or gray-green, narrowly alate adaxially; pinnae 6-11 pairs, in ours 2-7 cm. long and 0.8-1.8 cm. broad, sessile and narrow-adnate distally, the proximal ones short-stalked, approximate, slightly ascending, elliptic to lanceolate, often falcate, obtuse or subacute to somewhat attenuate, inequilateral at base, basiscopically cuneate or excavate, acroscopically truncate and occasionally subauriculate, the margins 2-serrate; veins 1- to 2-forked, mostly indistinct, the tips slightly enlarged, ending short of the margin; sori inframedial, linear to narrow-elliptic, often curved, 3-7 mm. long, 0.5-1.5 mm. broad; indusium delicate, linear, yellow to brownish or hyaline, subentire.

Martens and Galeotti described *A. polymorphum* from Mexico, based on precociously fertile juvenile specimens of *A. abscissum*. I have examined the type of the former, as well as a few similar specimens from Alta Verapaz and the West Indies. All are diminutive plants, from 4-11 cm. long, with two to five pairs of obtuse to subacute pinnae, many of which bear two to four relatively normal pairs of sori. However in all other features—rhizome scales, lamina outline, pinna margins, texture, and color—they are *A. abscissum*.

Asplenium achilleifolium (Mart. & Gal.) Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 249 (seors. 97) 1849 (not [Lam.] C. Chr. 1905). *Caenopteris achilleifolia* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 63, t. 16. 1842. *Athyrium achilleifolium* (Mart. & Gal.) Fée, Mém. Fam. Foug. V (Gen. Fil.): 186. 1850-52. *Asplenium grande* Fée, *op. cit.* VIII: 82. 1857 (not Sw. 1806) *A. achilleifolium* var. *pinnatifido-serratum* Hook. Sp. Fil. 3: 230. 1860. *Athyrium grande* (Fée) Fourn. Mex. Pl. 101. 1872. *Palma de tierra* (fide Steyermark, Quezaltenango).

On slopes in deep forests, in wet thickets, or on banks of wooded ravines, 1,100-2,500 m.; Alta Verapaz; Huehuetenango; El Quiché; Quezaltenango; San Marcos; Santa Rosa; Sololá; Suchitepéquez; Zacapa. Southern Mexico; Honduras; El Salvador; Nicaragua.

Plants terrestrial; rhizome stout, erect or ascending, amply provided with dark-brown, ovate or lanceolate, subentire scales, most of these 1-3 mm. broad, obscurely

clathrate, the cells crowded and their walls thick; leaves to nearly 1 m. long and 0.3 m. broad, pinnate-pinnatisect (nearly 2-pinnate), caespitose; petiole stout, nearly equaling, but commonly much shorter than, the lamina, light gray to greenish brown, terete abaxially, sulcate to trisulcate adaxially, sparsely scaly, the basal scales broad as on the rhizome, those toward the lamina widely scattered, tortuous and attenuate, apparently spinulose-dentate, mostly single-ribbed; lamina firm-herbaceous, ovate to lanceolate, tapering to a pinnatifid apex, slightly or not at all reduced at base, the tissue glabrous; rachis gray, green, or yellowish, glabrous, or sparsely and minutely scaly as on the upper petiole, lacking proliferous buds; pinnae numerous, 8-15 cm. long, slightly ascending, crowded to subdistant, sessile, truncate and narrowly decurrent at base, attenuate at apex, cut nearly to the costa; secondary segments 10-16 pairs, decurrent and forming a broad wing along the costa, serrate, or if lobed the acute lobes 3-5 pairs, nearly as broad as long; veins simple or apically forked in each of the ultimate segments, raised and distinct on both surfaces; sori 1 to each ultimate segment, broadly elliptic, mature ones to 3 mm. long and 2 mm. broad, diverging from the midrib at a wide angle; indusium thin, yellowish to whitish, elliptic, commonly 2 mm. long and 1 mm. broad.

Asplenium achilleifolium is easily confused with *A. solmsii*, which is a smaller fern with narrower segments and rhizome scales. In fact, the two probably differ from each other to a lesser degree than from several Mexican specimens found in the Field Museum herbarium. The latter specimens, from Jalisco and Veracruz, are certainly *A. achilleifolium*, but they all differ in some minor characters. The sori are mostly distal (*i.e.*, there are rarely any borne on the one to two proximal pairs of veins), the lamina is somewhat to strongly reduced at base, and the rachis scales are very abundant, many of these broad and distinctly clathrate—very similar to the scales of *A. commutatum*. These specimens may be worthy of varietal distinction, and such variation might be expected in the future among Guatemalan collections. Also in the Field Museum herbarium are several specimens from Nicaragua, Costa Rica, and Panama which have been identified as *A. solmsii* or *A. achilleifolium*. These are subtripinnatifid, with the same broadly alate costae, general leaf configuration, and texture that characterize the species complex. But the laminae are much more highly dissected than in typical *A. achilleifolium*, and the scales and indusia (where found) much larger than those of typical *A. solmsii*.

Thus there appears to be an aggregate of species or varieties in Mexico and Central America (probably including *A. commutatum*) which requires further and more detailed examination. Besides having broadly alate, bipinnatifid pinnae and dareoid sori, these plants all bear rather unique scales on the rachis and (sometimes) costae. The scales of *A. commutatum* are ample and obviously clathrate, with large, clear lumina (fig. 11e), but each cell along the scale margin lacks a marginal wall. Therefore, the two lateral walls project sharply and horizontally (still connected by the membrane), giving the scale a

spinulose-dentate appearance. These scales, especially on the lower rachis, are broad at base and taper to a usually attenuate and single-ribbed apex. Further up the rachis, the scales are often greatly narrowed, consisting only of a single, sinuous rib, with the short, projecting, lateral cell walls and connecting membrane. On the Jalisco and Veracruz specimens mentioned above, the rachis scales are quite similar. But on most specimens of *A. achilleifolium* and *A. solmsii* the rachis bears only the narrow scale with a single rib. Thus although the two extremes superficially (and under low magnification) may appear as two different scales, the single-ribbed scale is merely a greatly reduced form of the broad, clathrate type.

Asplenium alatum H. & B. ex Willd. in L. Sp. Pl. ed. 4, 5: 319. 1810.

In forests, on steep slopes, along ridges, or in wooded ravines, 1,300-2,700 m.; Alta Verapaz; San Marcos. Southern Mexico; Nicaragua to Colombia and Venezuela, south to Bolivia and Brazil.

Plants terrestrial; rhizome erect, provided with a few, dull-brown, ovate scales, these to 2 mm. long, obscurely clathrate (the cells small and isodiametric), commonly early-deciduous; leaves pinnate, crowded to subfasciculate, to 35 cm. long, 6-12 cm. broad; petiole 5-12 cm. long, about $\frac{1}{2}$ as long as the lamina, dull gray or gray-brown, with a few dull-brown, ovate scales near the base, abaxially terete, adaxially flattened and conspicuously green-alate, the wings 1-2 mm. broad; lamina broad-lanceolate or -oblong, glabrous, firm-membranaceous, scarcely reduced at base, rather abruptly terminating in a short-ligulate (apparently not rooting) tip which bears a proliferous bud; rachis glabrous, dull grayish, conspicuously green-alate; pinnae 12-20 pairs, to 7 cm. long and 1.5 cm. broad, sessile, subdistant, horizontally spreading, obtuse to acute, broadly cuneate at base, subequilateral, or scarcely auriculate acroscopically at base, the margin biserrate (often obtusely so); veins 1- or 2-forked, distinct, the tips not or scarcely enlarged, ending in the teeth short of the margin; sori inframedial, linear, about 5-8 mm. long; indusia linear, yellowish to green, thin, entire.

Asplenium auriculatum Sw. Kongl. Vetensk. Acad. Hand. 68. 1817 (not [Thunb.] Kuhn, 1868).

In forests, on slopes, or in wooded ravines, commonly on tree trunks or stumps, rarely on mossy rocks or rocky banks, 350-2,700 m.; Alta Verapaz; Baja Verapaz; Escuintla; El Progreso; Quezaltenango; El Quiché; San Marcos; Zacapa. West Indies; Mexico; Honduras to Panama; Colombia to Trinidad, south to Brazil and Bolivia.

Plants epiphytic, very rarely terrestrial or epipetric; rhizome erect, the apex bearing a thick cluster of castaneous, rather lustrous, lanceolate to ovate, clathrate scales, these 2-5 mm. long, 0.5-1 mm. broad; leaves pinnate, subfasciculate, 12-35 cm. long, 2.5-7 (8) cm. broad; petiole 3-12 cm. long, $\frac{1}{4}$ - $\frac{1}{2}$ as long as the lamina, with scales at or near the base as on the rhizome, greenish or gray to dull brown, terete or somewhat flattened, often marginate near the lamina; lamina lanceolate, glabrous, thin- to firm-mem-

branaceous, opaque, slightly or not at all reduced at base, rather abruptly terminating in a serrate-ligulate or indefinite apex, not proliferous; rachis glabrous, gray, green, or yellow-brown, marginate or narrow-alate; pinnae 9-14 (16) pairs, 1-4 cm. long and 0.4-1.2 cm. broad, short-stalked, commonly wide-spaced, horizontally-spreading, acute or sub-acute (rarely acuminate), oblong or oblong-lanceolate, often subfalcate, inequilateral at base, basiscopically cuneate or excavate, acroscopically truncate, commonly auriculate, the auricles often crowding or overlapping the rachis, the margins serrate or crenate-serrate; veins indistinct or (more commonly) obscure, those of the acroscopic side 1-forked, the basal one 2-forked, the distal ones and those of the basiscopic side simple, the tips not or scarcely enlarged, ending short of the margin; sori inframedial, linear to elliptic, straight, 2-5 mm. long, 0.6-1 mm. broad; indusium firm, fleshy, yellow or green to light brown, often revolute, subentire.

With this should probably be included *A. hastatum* Klotzsch ex Kze., of South America, which is presumed to differ only in size of auricles and width of rachis wings. Both taxa, with the closely related *A. salicifolium* L., are in need of further study.

***Asplenium auritum* Sw. J. Bot. (Schrader) 1800 (2): 52. 1801.**

Plants commonly epiphytic (very rarely reported as terrestrial or epipetric); rhizome erect, stout, provided with lanceolate or ovate, dark-brown to grayish brown, clathrate scales, these 2-4 mm. long, not attenuate; leaves pinnate to pinnate-pinnatisect, sub-caespitose, (in ours) 13-70 cm. long and (2) 3-15 cm. broad; petiole rather stout, narrow-marginate above (in ours), 5-30 cm. long, subequal to or about $\frac{1}{2}$ the length of the lamina, not or scarcely lustrous, abaxially terete, green or gray to red-brown, or (rarely) dull blackish, adaxially sulcate and often green, sparsely scaly near the base, frequently with a few, scattered, minute, blackish hairlike scales above; lamina lanceolate to oblong or narrowly subdeltoide, pale or yellowish green, chartaceous to subcoriaceous, not reduced at base, gradually terminating in a pinnatifid to serrate, sometimes attenuate, apex, not proliferous; rachis glabrous, or provided with a few scattered, minute, blackish, hairlike scales, green, gray or reddish brown, not alate or only narrowly so (at least in ours); pinnae 10-25 pairs, 2-9 cm. long, 0.4-1.6 cm. broad, many (or at least the proximal ones) short-stalked, approximate or (more commonly) widely spaced, ascending, lanceolate to linear-lanceolate, obtuse or acute to caudate, inequilateral at base, basiscopically cuneate or narrowly rounded, acroscopically truncate, subentire to pinnatifid (rarely nearly 2-pinnate as to the bases of proximal pinnae); veins 1- or 2-forked, or pinnate in basal auricles, indistinct or obscure, the tips slightly enlarged, ending short of the margin; sori inframedial, elliptic (often broadly so), frequently confluent at maturity, 3-4 mm. long, 1-2 mm. broad, borne at a narrow angle, and often appearing subparallel to the midrib; indusium relatively thick and fleshy, linear, yellow to whitish, subentire.

This is perhaps the most variable species in the genus and one of the most in need of monographic study. In its aggregate sense it is rather easy to recognize, for its leaves are commonly rather fleshy, and of a light, yellow-green color, which provides a striking background for the oval, rich-brown sori. The latter are relatively large, borne in lines nearly subparallel with the midrib, and are often confluent at maturity, so that frequently they nearly cover the abaxial side of the pinnae. The

plants are almost always epiphytic, with many leaves borne in fascicles from a rather stout rhizome. However, the inconsistency within the species complex lies in the degree of dissection of the leaves. In the simplest form, the lamina is merely pinnate, with the pinnae subentire, but in the most complex form it is tripinnate-pinnatifid, with ultimate segments minute and linear. Dozens of taxa have been proposed in various floristic treatments in an attempt to account for the often nebulous and nearly infinite intermediate conditions which have been observed or imagined by past workers. Unfortunately, most new species or varieties described in aggregate species such as this often only add to the confusion. A workable solution can be proposed only when collections have been assembled from all over the neotropics and exhaustive field and greenhouse studies have been made. As an example: in the field I have observed two leaves, borne on the same rhizome, one with subentire pinnae, the other with rather deeply lobed pinnae; and, growing alongside this plant on the same branch (but from a different rhizome) was another plant, with laminae pinnate-pinnatifid to bipinnate-pinnatifid.

For the present treatment, in a purely arbitrary decision, I recognize two species in Guatemala: *A. auritum* (including three varieties), and *A. cuspidatum* (including four varieties). A key to the two species follows:

Pinnae simple and entire to pinnatifid (rarely nearly 2-pinnate as to bases of proximal pinnae); basal segments (if any) adnate, never truly stalked. *A. auritum*.
 Pinnae (at least the proximal ones) pinnate to nearly 3-pinnate; basal segments (pinnales) of proximal pinnae obviously stalked. *A. cuspidatum*.

Asplenium auritum* var. *auriculatum (Hook. *fil.*) Morton & Lell.
 Mem. New York Bot. Gard. 15: 19. 1966. *A. marinum* L. var. *auriculatum* Hook. *fil.* Trans. Linn. Soc. London 20: 170. 1847. *A. monodon* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 249 (seors. 95). 1849. *A. auritum* var. *monodon* (Liebm.) Fourn. Mex. Pl. 1: 106. 1872.

In forests or thickets, on branches or trunks of trees or on fallen logs (very rarely on the forest floor), 0-900 m.; Alta Verapaz; Escuintla; Izabal; Petén; El Quiché; Retalhuleu; San Marcos; Suchitepéquez. Greater Antilles; southern Mexico; British Honduras; Honduras to Panama; Colombia to Trinidad; Ecuador; Peru.

Mature leaves 13-60 cm. long, (2) 3-8 (10) cm. broad; rachis narrowly alate distally; pinnae obtuse to acute, subentire to biserrate, a basal acroscopic auricle lacking or low and obtuse, often dentate, separated from the rest of the pinna by a shallow sinus, or the sinus lacking.

A number of Guatemalan specimens may be found in herbaria determined as *A. erosum* L., or *A. auritum* var. *serratum* Bak.

***Asplenium auritum* var. *auritum*.** ?*Polypodium serratum* Aubl. Pl. Guiane 2: 972. 1775 (not *A. serratum* L. 1753). *A. sulcatum* auctt. (not Lam. 1786).

In forests or thickets, on branches or trunks of trees or on fallen logs (rarely reported on mossy rocks), 70-2,000 m.; Alta Verapaz; Baja Verapaz; Escuintla; Izabal; Petén; El Progreso; Quezaltenango; El Quiché; Retalhuleu; San Marcos. Southern Florida; Greater Antilles; southern Mexico; British Honduras; Honduras to Colombia and Venezuela, southward to Brazil and Bolivia.

Mature leaves 13-60 cm. long, 3-11.5 (-15) cm. broad; rachis nonalate or essentially so; pinnae mostly acute to caudate, with margins bicrenate-serrate, or rarely with a few shallow lobes, basal acroscopic auricle (at least on proximal pinnae) prominent, often acute, separated from the rest of the pinna by a deep or moderately deep sinus.

For a more detailed discussion of the nomenclature and synonyms of *A. auritum*, see Morton & Lell. (1966).

Asplenium auritum* var. *bipinnatifidum Kunze, Linnaea 18: 332. 1844. *A. rigidum* Sw. Kongl. Vetensk. Acad. Handl. 68: 1817. *A. auritum* var. *bipinnatisectum* Mett. Abh. Senckenberg Naturf. Ges. 3: 147. 1858.

In forests, thickets, or clearings, on trunks of trees or fallen logs, 350-1,800 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Petén; El Quiché; San Marcos; Suchitepéquez. Greater Antilles; Mexico; Honduras; Costa Rica to Colombia and Venezuela, southward to Bolivia and Argentina.

Mature leaves 16-70 cm. long, 4-15 cm. broad; rachis nonalate or essentially so; pinnae acute to caudate, mostly pinnatifid, the basal acroscopic segment (and often others) commonly deeply incised, often nearly free (but not stalked).

Asplenium breedlovei A. R. Smith, Proc. Calif. Acad. Sci. 40: 209. 1975 (type from Chiapas: municipio Villa Corzo, east base of Cerro Tres Picos, 1,500-1,800 m., *Breedlove 30041*).

In wet places, usually on slopes of volcanoes, along creeks, waterfalls, and on banks of ravines, 1,200-1,800 m.; Chimaltenango; Quezaltenango; San Marcos; Santa Rosa. Mexico (Chiapas).

Plants terrestrial; rhizome short-creeping, provided with minute, dark-brown, clathrate, lanceolate or ovate scales about 1 mm. long; leaves 20-40 cm. long, 6-15 cm. broad, 3-pinnate-pinnatifid, approximate to crowded on the rhizome; petiole stout, 1.2-2 mm. thick, nearly as long as the lamina, reddish or greenish brown, not lustrous, glabrous, nonalate, terete abaxially, sulcate adaxially; lamina glabrous, thin- to firm-herbaceous, ovate or (more commonly) deltoid, gradually reduced to a pinnatifid, sometimes atten-

uate apex, not reduced at base; rachis not proliferous, reddish or greenish brown, nonalate (or scarcely alate near apex); pinnae 8-16 pairs, to about 10 cm. long, crowded to imbricate, ascending, stalked, the costa not alate, or only narrowly so near the apex; pinnules (of larger pinnae) 6-10 pairs, commonly stalked, cut deeply or quite to the base into 2-3 pairs of segments; ultimate segments cuneiform, with 2-5 subacute lobes; veins simple in the lobes, distinct, the tips not or scarcely enlarged, terminating just short of the margin; sori 1-3 in the penultimate segments, narrow-elliptic, 2-3 mm. long and 0.2-0.6 mm. broad; indusia linear, entire or slightly erose, delicate, yellowish.

Asplenium castaneum Schlecht. & Cham. *Linnaea* 5: 611. 1830.
A. rubinum Dav. Bot. Gaz. 19: 391. 1894.

In high forests, commonly on rocks or in rocky crevices, rarely on mossy banks or on tree trunks, 2,400-4,100 m.; Huehuetenango; Quezaltenango; Sacatepéquez; San Marcos; Sololá. Southern Mexico (type from Mt. Orizaba, Veracruz, *Schiede & Deppe s.n.*); Costa Rica; Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Plants epipetric, rarely epiphytic; rhizome short, stout, amply provided with ovate, brown, clathrate, translucent scales, the broad, clear cells of which are essentially uniform, the cell walls thin; leaves numerous, erect, densely caespitose, to 30 cm. long and less than 2 cm. broad; petiole 3-12 cm. long, shorter than the lamina, terete (but appearing slightly flattened adaxially due to the presence of 2 minute parallel ribs), lustrous, dark brown to (rarely) atropurpureous, nonalate, sparsely provided with dark, fibrillose scales; lamina glabrous, simply pinnate, firm-herbaceous to chartaceous, linear, gradually reduced to base, and diminished to a minute, terminal "pinna"; rachis terete, dark brown to atropurpureous, sparsely provided with dark, fibrillose scales, rarely proliferous near apex, provided adaxially with thin cartilaginous ribs which commonly become perpendicular wings distally; pinnae 10 to many pairs, 3-10 mm. long, 2-5 mm. broad, 1-2 times as long as broad, patent, elliptic to broadly oblong or subquadrangular, short-stalked, the stalks commonly bicolorous, essentially green, but irregularly deciduous from a short, raised, castaneous base, margins entire to crenate; veins obscure or indistinct, terminating short of the margin in enlarged hydathodes, which are conspicuous adaxially; sori rarely solitary on the basiscopic side (especially on distal pinnae), but more commonly borne in 2-4 pairs, these often confluent at maturity; indusium relatively large and broad, pale green to whitish, entire to erose, persistent, but often obscured at maturity by the numerous, spreading sporangia.

It is with some reluctance that I have maintained this as a species distinct from *A. monanthes*. It might be more validly considered a variety. Previous authors have separated the two by the "main" characters of rhizome scales, number of sori, margins of indusia, pinna shape, and leaf size. Of these, rhizome scales and pinna shape are the most reliable characters in Guatemala. The pinnae of *A. castaneum* are commonly almost as broad as long, and the rhizome scales are broad, obviously clathrate and translucent, while *A. monanthes* has narrow, elongated pinnae and linear, opaque rhizome scales with relatively thick cell walls. However, numerous Guatemalan collections have been examined on which these characters are inconsistent or

intermediate. With these specimens, the only recourse is to classify them by use of the largest combination of characters.

During my research on this group, one new character has come to light, which hitherto seems to have gone unnoticed—a minute feature which is about as reliable as any other. The tapered base of the pinna, which might be considered a “stalk,” is uniformly green in *A. monanthes*, all the way from the surface of the rachis, where it often arises from a circular depression. Thus the pinna base often appears nodose-articulate. In *A. castaneum* there is never a circular depression and the pinna “stalk” is often bicolorous, the brown coloration abruptly changing to green just below the pinna base. In many specimens examined where some of the pinnae have fallen or broken off, the separation has occurred at this color line, and the rachis is then muricate with these dark-brown pinna bases.

***Asplenium commutatum* Mett. ex Kuhn, Linnaea 36: 99. 1869.**
Culandrillo (*vide* Steyermark, Quezaltenango).

Growing in deep, wet forests, commonly on mountain slopes or banks of ravines, 2,000-3,500 m.; Chimaltenango; El Progreso; Quezaltenango; El Quiché; San Marcos. Mexico; El Salvador to Panama; Haiti.

Plants terrestrial; rhizome stout, ascending or erect, amply provided with castaneous to light-brown, clathrate scales, these lanceolate to ovate, entire, thin and somewhat flaccid; leaves nearly 1 m. long and 20 cm. broad, 2-pinnate-pinnatifid, crowded to caespitose; petiole much shorter than the lamina, terete abaxially, 2- or 3-sulcate adaxially, dull, grayish or yellowish brown, sparsely to amply scaly, the scales near the base like those on the rhizome, but toward the lamina becoming longer and narrower, the margins appearing spinulose-dentate, the tips often single-ribbed and attenuate; lamina firm-herbaceous, lanceolate, tapering to a pinnatifid apex, slightly reduced at base, the tissue glabrous; rachis (and often the costa) amply spinulose-scaly as on the upper petiole, commonly with a proliferous bud at the apex; pinnae numerous, medial ones 5-8 cm. long, spreading to slightly ascending, crowded to subdistant, sessile, the basal pinnules often overlapping the rachis, the apex acuminate; pinnules about 8-12 pairs, obtuse, narrowly adnate to the alate costa, commonly deeply lobed, the larger ones with 3-4 pairs of ultimate segments; veins simple to 1-forked in the segments; sori diverging from the midrib at a rather broad angle; indusium yellowish to whitish, often thin and translucent.

With this should probably be placed *A. subvestitum* Copel., of Mexico, which does not appear to differ significantly.

Some authors have reported *A. bulbiferum* Forst. from southern Mexico and Guatemala. This is an Old World species which is similar to *A. commutatum*, but differs, among other features, in its entire and abruptly acute rachis scales. Those of *A. commutatum* appear spinulose-dentate, with attenuate, single-ribbed tips.

See *A. achilleifolium* for additional discussion.

Asplenium cristatum Lam. Encycl. Méth. Bot. 2: 310. 1786. *A. cicutarium* Sw. Prodr. Veg. Ind. Occ. 130. 1788. *A. dissectum* Link. Hort. Reg. Bot. Berol. Descr. 2: 68. 1833 (not Sw. 1788).

In forests, thickets, or shaded ravines, on rocks, tree trunks, or the forest floor, 100-700 (-1,800) m.; Alta Verapaz; Izabal; Petén; Sololá; Santa Rosa. Florida; West Indies; Mexico to Colombia and the Guianas, and south to Brazil and Bolivia.

Plants terrestrial, epipetric, or epiphytic; rhizome erect, provided at apex with small, dark-brown, lanceolate, attenuate scales, these obviously clathrate, their cells broad and clear; leaves to 40 (60) cm. long and 12 (15) cm. broad, 2-pinnate or 2-pinnate-pinnatifid (rarely nearly 3-pinnate), caespitose; petiole wiry, about 1 mm. thick, nearly as long as the lamina, gray to greenish or reddish brown, not lustrous, glabrous, terete abaxially, conspicuously green-alate and sometimes shallowly sulcate adaxially; lamina glabrous, firm-membranaceous, lanceolate to oblong, 1.2-1.6 times as long as the petiole, gradually reduced to a pinnatifid, often attenuate apex, scarcely or not at all reduced at base (or rarely 1-4 lower pairs of pinnae substantially reduced); rachis not proliferous, gray or yellowish to reddish brown, green-alate; pinnae 15-20 pairs, crowded to imbricate, larger ones 4-7 cm. long, approximate to imbricate, the basal pair (rarely 1-4 pairs) sometimes reduced and deflexed, most of them borne at right angles to the rachis, sessile, the basal pinnules commonly overlapping the rachis, costae alate, the wings extending out along the bases of pinnules adaxially; pinnules about 10 pairs (on larger pinnae), subsessile or rarely short-stalked, most of them narrowly adnate to the costal wing, broadly oblong, lobed or deeply incised, the 2-3 pairs of segments acute; veins mostly simple in the segments, distinct, the tips not enlarged, terminating short of the margin; sori 3-8 on a pinnule, elliptic, 1-2 mm. long, 0.6-0.8 mm. broad; indusia narrow-elliptic, grayish to yellowish, delicate, entire to slightly erose.

In Guatemala, *A. cristatum* is commonly quite consistent, in morphological features as well as in geographic limits. Laminae are scarcely or not at all reduced at base, pinnae and pinnules are sessile, and collections have been made at altitudes of 100-700 m. in the contiguous departments of Alta Verapaz, Petén, and Izabal. However, two specimens have been collected (*Steyermark 48009*, *Heyde & Lux 4675*) which tend to approach *A. myriophyllum*, in that the laminae are more strongly reduced at base and more deeply dissected, and pinnules are mostly short-stalked. The Steyermark collection was made in Sololá at about 1,000 m., the Heyde and Lux collection in Santa Rosa at 1,800 m. There appear to have been even more intermediate plants collected in southern Central America and the West Indies, so a careful study of the entire complex will be needed to clarify relationships. (See also *A. myriophyllum* for further discussion.)

The following supplementary key may be of help in distinguishing the two species, as they occur in Guatemala:

Lamina not or scarcely reduced at base, 1.2-1.6 times as long as the petiole; mature leaves (10) 12-40 (60) cm. long; pinnules usually crowded to imbricate; commonly at 100-700 m. alt. *A. cristatum*.
 Lamina conspicuously reduced at base, (1.5) 2-6 times as long as the petiole; leaves to 11 cm. long; pinnules usually approximate to subdistant; commonly at 900-1,600 m. alt. *A. myriophyllum*.

***Asplenium cuneatum* Lam. Encycl. Méth. Bot. 2: 309. 1786.**

Of Guatemalan specimens, I have seen only a fragment of *Warczewicz s.n.* (exact locality unspecified), and *Contreras 4863* (epiphyte, Dept. Alta Verapaz, Chapultepec Farm, 62 km. from Cobán, in forest bordering arroyo). The species is also terrestrial or epipetric, as well as epiphytic, at altitudes from 100-1,000 m. in Honduras; Nicaragua; Costa Rica; West Indies; Colombia to the Guianas; Brazil and Peru; Africa; Polynesia.

Rhizome ascending or short-creeping, provided with dark-brown, clathrate, linear scales to 5 mm. long; leaves to 60 cm. long and 15 cm. broad, nearly 3-pinnate, crowded to subcaespitose; petiole somewhat shorter than the lamina, reddish to yellowish brown, not or scarcely lustrous, glabrous (or with a few, scattered filamentous scales), terete abaxially, sulcate adaxially; lamina glabrous, chartaceous, opaque, oblong-lanceolate, gradually reduced to a pinnatifid and often attenuate apex, scarcely or not reduced at base; rachis not proliferous, reddish or yellowish brown, nonalate, or with very narrow, inconspicuous wings distally; pinnae 12 to many pairs, 3-12 cm. long, subdistant, ascending, obviously stalked, the costa nonalate; pinnules (of larger pinnae) 3-8 pairs, at least the proximal ones short-stalked, broadly dentate to lobed, or the basal ones cut nearly or quite to the costule into 1 or 2 pairs of segments; ultimate segments obovate, broadly and obtusely dentate toward the apex; veins immersed and indistinct, subflabellate, commonly forked; sori usually 3-5 on the segments, linear, borne on the veins, at a very narrow angle (often subparallel) to the costule; indusium yellowish, firm, often revolute.

***Asplenium cuspidatum* Lam. Encycl. Meth. Bot. 2: 310. 1786.**

Plants commonly epiphytic, rarely terrestrial or epipetric; rhizome erect, stout, provided with lanceolate or ovate, dark-brown to gray-brown, clathrate scales, these 2-4 mm. long, not attenuate; leaves 2-pinnate (at least as to basal pinnae) to nearly 4-pinnate, caespitose, 4-50 cm. long, 2-18 cm. broad; petiole delicate to stout, nonalate, 2-25 cm. long, subequal to, or about $\frac{1}{2}$ the length of, the lamina, not or scarcely lustrous, abaxially terete, green or gray to red-brown, or dull blackish, adaxially sulcate and often green, sparsely scaly near the base, frequently with a few, scattered, minute, blackish hairlike scales above; lamina lanceolate to ovate or subdeltoid; commonly pale or yellowish green, firm-membranaceous to chartaceous, not reduced at base, gradually terminating in a pinnatifid to serrate, often caudate, apex, not proliferous; rachis glabrous, or provided with a few scattered, minute, blackish, hairlike scales, green, gray, or reddish brown, nonalate, or narrowly so or marginate toward the apex; pinnae 6 to many pairs, 1-8 cm. long, most of them stalked, approximate to widely spaced, ascending, linear-lanceolate to ovate, acute to caudate, the base more strongly produced acroscopically; pinnules subentire to serrate to nearly 3-pinnate, at least the basal ones of proximal pinnae obviously stalked, lanceolate, ovate, or elliptic; veins simple or forked to

pinnately branched, indistinct or obscure, the tips slightly enlarged, ending short of the margin; sori commonly inframedial, narrowly to broadly elliptic, in more highly dissected laminae often extending beyond the edges of narrower segments; indusium relatively thick and fleshy, linear, yellow, grayish or whitish, subentire.

This and *A. auritum* are difficult to separate, and then only in an arbitrary manner. A key and detailed discussion of the problems may be found under the latter species. As in *A. auritum*, the varieties of *A. cuspidatum* are based on the degree of dissection of the leaves. The following four varieties are recognized in Guatemala.

***Asplenium cuspidatum* var. *cuspidatum*.**

In forests or wooded ravines, on tree trunks or fallen logs, or rarely on moss-covered rocks, 350-3,000 m.; Alta Verapaz; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez; San Marcos. West Indies; Mexico; Honduras; Nicaragua to Colombia and Venezuela, south to Bolivia and Brazil; Argentina.

Mature leaves (10) 12-50 cm. long; petiole (0.4) 0.6-1.5 mm. thick; lamina commonly pinnate-pinnatifid, or 2-pinnate as to the basal segments of lower pinnae; pinnules subentire to mostly serrate, 0.8-2.2 mm. broad.

A new species, *A. sphaerosporum* A. R. Smith (Amer. Fern J. 70: 17. 1980), was published while this *Flora* was in press. The two Guatemalan specimens cited by Smith are included here.

***Asplenium cuspidatum* var. *foeniculaceum* (HBK) Morton & Lell., Mem. New York Bot. Gard. 15: 29. 1966. *A. foeniculaceum* HBK, Nov. Gen. & Sp. 1: 15. 1815. *A. fragrans* Sw. var. *foeniculaceum* (HBK) Hook. Sp. Fil. 3: 181. 1860.**

In forests or wet, wooded ravines, on trees or tree stumps, 350-2,700 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; El Quiché; San Marcos. Mexico; El Salvador; Costa Rica to Colombia and Venezuela, south to Bolivia and Brazil.

Mature leaves 12-50 cm. long; petiole 0.6-1.5 mm. thick; lamina commonly 3-pinnate to nearly 4-pinnate; pinnules decompose, most of them stalked, the tertiary segments commonly stalked (at least those on proximal pinnules); ultimate segments 0.4-1.5 mm. broad; mature sori on the narrower segments often extending over the segment margin.

***Asplenium cuspidatum* var. *tenerrimum* (Mett.) Morton & Lell. Mem. New York Bot. Gard. 15: 29. 1966. *A. tenerrimum* Mett. ex Kuhn, Linnaea 36: 97. 1869. (?) *A. fournieri* Kuhn ex Fourn. Bull. Soc. Bot. France 17: 237. 1870.**

On tree trunks in forests, 250-350 m.; Alta Verapaz. (Nicaragua?); Costa Rica; Colombia; Venezuela.

Mature leaves 4-9 cm. long; petiole delicate, 0.2-0.4 mm. thick; lamina 2-pinnate to (at

base) 3-pinnate; pinnules mostly stalked, with ultimate segments 0.4-0.7 mm. broad; mature sori commonly spreading over the segment margin.

Although apparently found in Guatemala only as an epiphyte, this variety has been reported in Costa Rica and Venezuela also on wet rocks and stream banks. *Asplenium fournieri* of Nicaragua may also belong here, although I have not seen the type.

Asplenium cuspidatum* var. *tripinnatum (Fourn.) Morton & Lell., Mem. New York Bot. Gard. 15: 29. 1966. *A. fragrans* Sw. Prodr. Veg. Ind. Occ. 130: 1788. *A. auritum* var. *tripinnatum* Fourn. Mex. Pl. 1: 107. 1872.

In deep shade of wet forests, commonly on trees or stumps, but rarely on wet banks or mossy rocks, 700-2,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Izabal; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Suchitepéquez; Zacapa. Greater Antilles; Mexico; Honduras to Panama; Colombia and Venezuela, south to Brazil and Bolivia.

Mature leaves (10) 12-50 cm. long; petiole 0.8-2 mm. thick; lamina commonly 2-pinnate-pinnatifid to (at base) subtripinnate; pinnules mostly stalked, at least the lower ones of larger pinnae lobed nearly or quite to the costule; tertiary segments adnate, rarely or never stalked; ultimate segments 0.7-2 mm. broad.

Asplenium delitescens (Maxon) Gómez, Brenesia 8: 52. 1976. *Diplazium delitescens* Maxon, Contr. U.S. Natl. Herb. 10: 497. 1908.

In wet forests, commonly on ridges or hillsides, 50-350 m.; Alta Verapaz; Petén; Retalhuleu. Cuba; southern Mexico; British Honduras; Honduras to Panama; Colombia (?); Ecuador (?); Peru.

Plants terrestrial; rhizome short-creeping, dorsiventral, rather sparsely provided with dark brown to blackish (sometimes bicolorous), lanceolate, clathrate scales, these somewhat lustrous, entire, 1-2 mm. long; leaves pinnate, crowded on the rhizome, 30-50 cm. long, 15-24 cm. broad, the lamina nearly as broad as long; petiole wiry, 1.5-3 mm. thick, nearly as long as the lamina, dull red- to yellow-brown or greenish, somewhat flattened-quadrangular, provided with a few, scattered, lanceolate scales, these mixed with some minute, blackish, tortuous hairlike ones; lamina broadly oblong or subdeltoide, firm-herbaceous, scarcely or not reduced at base, abruptly reduced to a nonconform, often attenuate, apical segment, this deeply pinnatifid at base, serrate toward the tip, not proliferous; rachis greenish or yellowish, marginate or inconspicuously alate distally, sparsely provided with blackish, hairlike, tortuous scales; pinnae (5) 6-8 pairs, 5-12 cm. long, 1.2-2.2 cm. broad, sessile (or basal ones very short-stalked), widely spaced, horizontally to slightly ascending, lanceolate, attenuate, inequilateral at base, narrowly cuneate to excavate basiscopically, truncate (and sometimes subauriculate) acroscopically, crenate-serrate; veins 1- to 2-forked, distinct or indistinct, the tips not or slightly enlarged, ending short of the margin; sori linear, 5-14 mm. long, 1 mm. broad, curved, frequently double (diplazoid), often nearly extending from costa to margin; indusium linear, delicate, greenish or yellow-brown, subentire.

Asplenium dissectum Sw. Prodr. Veg. Ind. Occ. 130. 1788 (not Gmel. 1791, Link, 1833, nor Brack. 1854). *A. bissectum* Sw. J. Bot. (Schrader) 1800 (2): 55. 1801.

Apparently known from a single collection in Guatemala: on tree, alt. 2,500 ft., Quebradas Secas, Alta Verapaz (*H. Johnson 810*). Nicaragua; Costa Rica; Panama; Greater Antilles; Colombia; Venezuela; Ecuador; Brazil.

Plants epiphytic; rhizome short-creeping to ascending, amply provided with clathrate, gray-brown to blackish, linear-lanceolate, attenuate scales; leaves to 50 cm. long and 10 cm. broad, erect to spreading, crowded or subcaespitose; petiole much shorter than the lamina, terete, lustrous, dark brown to atropurpureous, sparsely provided with gland-tipped trichomes, and with a few scattered, linear or filiform scales; lamina pinnate-pinnatifid, firm-herbaceous, linear to lanceolate, tapering very gradually to a pinnatifid apex, essentially glabrous; rachis like the petiole but shallowly sulcate adaxially, not proliferous; pinnae numerous, to 8 cm. long, spreading to somewhat ascending, short-stalked, deeply lacerate, with a long-caudate apex and an inequilateral base, cuneate basiscopically and subauriculate acroscopically; veins commonly only 1-forked in the ultimate segments, ascending from the costa at a very acute angle; sori borne on veins adjacent to the costa at a narrow angle, often appearing nearly parallel to the costa; indusium brownish, long and narrow, often becoming hidden by the numerous, spreading sporangia at maturity.

Asplenium exiguum Bedd. Ferns So. India 49, t. 146. 1863. *Athyrium gracile* Fourn. Mex. Pl. 1: 102. 1872. *Asplenium glenniei* Bak. Syn. Fil. ed. 2: 488. 1874. *A. gracile* (Fourn.) Hemsl. Biol. Centr. Amer. 3: 634. 1885 (not Don, 1825 nor Fée, 1857).

In damp, shaded ravines, or on moist cliffs or mossy, rocky ledges, 1,000-2,000 m.; Huehuetenango. United States (Arizona); Mexico; India; China; the Philippines.

Plants terrestrial or epipetric; rhizome erect, provided with linear or lanceolate, clathrate scales, these gray-brown to blackish, to 1.5 mm. long, often attenuate; leaves pinnate-pinnatifid, densely caespitose, in ours 3-10 cm. long and 0.8-1.5 cm. broad; petiole wiry, 0.5-1.5 cm. long, much shorter than the lamina, flattened, somewhat scaly (scales linear at base, filiform above), green and narrowly sulcate adaxially, dark brown to atropurpureous and often lustrous abaxially, nonlate; lamina linear or oblong-lanceolate, thin- to firm-herbaceous, opaque, somewhat or not at all reduced at base, tapering gradually to a pinnatifid apex, or often with a short-caudate, proliferous tip; rachis marginate to narrow-alate, green and narrowly sulcate adaxially, green to dark brown and subterete abaxially, sparsely to amply provided with dark-brown, minute filiform scales, these 1-3 cells broad at base, but commonly with a single-ribbed, tortuous apex; pinnae (in ours) 6-14 pairs, 3-10 mm. long, 2-4 mm. broad, sessile, subopposite, widely spaced, horizontally spreading, the apex obtuse (often with a minute, proliferous bud), broadly cuneate at base, cut deeply (often nearly to costa) into 3-4 pairs of obtuse lobes, these often revolute, sometimes bifid; veins indistinct, simple to 1-forked, the tips not enlarged, terminating short of the pinna margin; sori inframedial, commonly 1 to a segment, 0.5-1 mm. long, relatively broad, and often confluent at maturity; indusium broad, yellow to whitish, subentire.

One of the most distinctive features of this species is its bicolorous petiole. It is terete or flattened on the abaxial side, and the shiny, usually dark-brown hue extends well up onto the rachis. However, the adaxial side is narrowly grooved and is bright green throughout.

This should be confused with no other species in Guatemala. Some Arizona and Mexican specimens of *A. exiguum* have been determined in herbaria as *A. fontanum* (L.) Bernh., a European species which is quite distinct, especially in its spinulose-tipped segments. *Asplenium exiguum* is rather rare in the New World, with a wide and interesting disjunction in distribution. This, along with synonyms and relationships, was discussed in detail in a fine paper by Hope (Bull. Torrey Bot. Club 26: 58. 1899).

Asplenium falcinellum Maxon, Contr. U.S. Natl. Herb. 13:14. 1909.

On tree trunks in forests, 300-900 m.; Alta Verapaz (type from Cubilguitz, 350 m., *Tuerckheim II-1910*); Izabal. Trinidad; Jamaica; southern Mexico; British Honduras; Honduras to Colombia.

Plants epiphytic; rhizome ascending or erect, with golden-tomentose roots and amply provided with lanceolate to linear, attenuate (often filiform and tortuous) lustrous brown scales, these to 5 mm. long, obscurely clathrate, the cells isodiametric at base, but greatly elongated toward the tips; leaves pinnate, crowded or subfasciculate, to 80 cm. long and 30 cm. broad; petiole stout, 1-4 mm. thick, 8-20 cm. long, about half as long as the lamina, dull gray or gray-brown, glabrous, abaxially terete, adaxially flattened or shallowly sulcate, nonalate; lamina ovate or elliptic, chartaceous, glabrous, scarcely reduced at base, terminating in a conform apical segment, not proliferous; rachis glabrous, dull grayish or gray-brown, nonalate; pinnae 5-10 (12) pairs, 6-16 cm. long and 1-2.5 cm. broad, stalked, widely spaced, slightly ascending, lanceolate, falcate, attenuate, subequally cuneate at base, the margins entire (rarely obscurely crenulate); veins 2- to 3-forked, commonly indistinct, their tips slightly enlarged, ending short of the margin; sori medial, linear, 5-20 mm. long; indusium yellow to green, fleshy, often revolute.

This is probably synonymous with *A. juglandifolium* Lam. of South America and *A. integerrimum* Sprengel of the West Indies, from which it is said to differ in its smaller and thinner pinnae. I have not seen the types of these two species, but judging from the original descriptions and the collections identified as such, there seems to be no reason to keep any of them separate. The name *A. juglandifolium* has priority. It may be confused with *A. tuerckheimii*, under which see further discussion.

Asplenium feei Kunze ex Fée, Mém. Fam. Foug. V (Gen. Fil.): 194. 1852. *A. sanguinolentum* Kunze ex Mett. Abh. Senckenberg Naturf. Ges. 3: 142, t. 4, f. 10. 1858.



FIG. 10. *Asplenium* (simply pinnate species). a, *A. repandulum*, habit, $\times \frac{1}{2}$; b, *A. radicans* var. *cirrhatum*, leaf apex, $\times \frac{1}{2}$; c, *A. laetum*, leaf apex, $\times \frac{1}{2}$; d, *A. pumilum*, habit, $\times \frac{1}{2}$; e, *A. pteropus*, portion of rachis and pinnae bases, $\times 3$; f, *A. williamsii*, pinna base, $\times 3$; g, *A. falcinellum*, pinna base, $\times 3$; h, *A. feei*, pinna base, $\times 3$.

Not yet reported from Guatemala, but to be expected there. In wet forests, on tree trunks or fallen logs, or occasionally on the forest floor, 500-1,800 m.; southern Mexico; Honduras and El Salvador to Bolivia and Brazil; Cuba; Hispaniola; Puerto Rico.

Plants terrestrial or, more commonly, epiphytic; rhizome erect or ascending, amply provided with light or dark brown, clearly clathrate, linear to lanceolate, long-attenuate scales, these (2) 3-7 mm. long, 0.3-1 mm. broad, usually with tortuous tips; leaves pinnate, approximate to subfasciculate, 25-60 cm. long, 6-15 (20) cm. broad; petiole stout, rather fleshy, 1-3 mm. thick, dull yellowish or reddish brown, occasionally atropurpureous (but never lustrous), somewhat flattened, shallow-sulcate adaxially, basally broad-paleate as on the rhizome, the scales becoming hairlike and sparse upward toward the lamina; lamina oblong-lanceolate, often broadly so, firm-herbaceous to chartaceous, not reduced at base, terminating in a conform apical segment, not proliferous, essentially glabrous, but costae and veins very sparsely provided with dark, minute, modified, hairlike scales; rachis glabrous or sparsely fibrillose-scaly, greenish or reddish brown, narrow-alate (at least distally); pinnae (5) 6-15 pairs, 4-12 cm. long, 1-2 cm. broad, short-stalked, widely spaced, ascending, lanceolate, acute or sometimes attenuate, slightly to strongly inequilateral at base, narrowly cuneate to somewhat excavate basiscopically, truncate and more strongly produced (often auriculate) acroscopically, margins crenate-serrate to biserrate; veins 1- to 2-forked, indistinct or obscure, the tips not at all enlarged, ending short of the pinna margin; sori strongly inframedial, elliptic or oblong, relatively broad, 3-5 mm. long, 1-1.5 mm. broad; indusium broad, translucent, delicate, yellowish or light brown, subentire.

There are several African species allied with or conspecific with *A. anisophyllum* Kunze. *Asplenium feei* certainly belongs to this complex, which is characterized by quite broad, inframedial sori, conform apical segments and attenuate, clathrate rhizome scales. The species in this complex are said to differ in the size of leaf and the depth of the serrations of pinnae, characters which are naturally variable and here not particularly significant. It may well be that all should be lumped under *A. anisophyllum*, the name which has priority.

Asplenium formosum Willd. in L. Sp. Pl., ed. 4, 5: 329. 1810. *Much-cōk* (Mayan, Petén, *vide* Cook & Martin).

In forests, thickets, or wooded ravines, on rocks or rocky slopes, commonly on fallen logs, and sometimes on tree trunks, 50-1,500 m.; Alta Verapaz; Chiquimula; Escuintla; Izabal; Jalapa; Petén; Retalhuleu; Santa Rosa. West Indies; Mexico to Colombia and Venezuela, south to Argentina and Paraguay; India; Ceylon; tropical Africa.

Plants terrestrial, epipetric, or occasionally epiphytic; rhizomes short, erect, provided with linear, rigid, bicolorous scales, these to 5 mm. long, obscurely clathrate, black, with narrow brown margins; leaves numerous, erect, caespitose, to 40 cm. long and nearly 3 cm. broad; petiole 0.5-4 cm. long, terete, lustrous, atropurpureous to black, glabrous, adaxially alate nearly or quite to base, the wings very narrow, partly deciduous; lamina glabrous, simply pinnate, firm-herbaceous to chartaceous, linear, tapering to a pinnatifid apex, gradually narrowed at base; rachis glabrous, not proliferous, commonly atropur-

pureous, terete, but often appearing adaxially sulcate due to the narrow wings which are frequently perpendicular to the rachis; pinnae very numerous, to 1.5 cm. long, patent, sessile, narrow and subacute, subdimidiate, basiscopically cuneate at base, and the margin entire to biserrate, acroscopically truncate, auriculate, the margin deeply biserrate or sharply lobed, basal ones commonly reduced to mere auricles; veins indistinct, obliquely spreading from a thin, ill-defined costa, simple or 1-forked, tips not enlarged, terminating short of the plane, segment margin; sori commonly 1-3, mostly borne on the distal and basiscopic portion of pinnae, elliptic to ovate, often confluent at maturity; indusium relatively large, pale green to whitish, subpersistent.

Reported by Cook and Martin to be used in Petén as a remedy for the common cold (perhaps prepared as a tea).

Asplenium harpeodes Kunze, Linnaea 18: 329. 1844. *A. donnell-smithii* Christ, Bot. Gaz. 20: 544. 1895 (type from Nebaj. El Quiché, Heyde & Lux s.n. [ed. Donn.-Sm. 4678]).

In dense wet forests and wooded ravines, usually pendent from tree trunks, 1,500-2,850 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Quezaltenango; El Quiché; San Marcos; Zacapa. Greater Antilles; southern Mexico; El Salvador; Honduras to Colombia and Venezuela, south to Bolivia and Brazil.

Plants epiphytic; rhizome short, erect, densely covered at the apex with linear, lustrous, dark or reddish brown, clathrate scales, these to nearly 1 cm. long, commonly long-attenuate, with tortuous tips; leaves pinnate, densely caespitose, mature ones 30-80 cm. long, 4-12 cm. broad; petiole stout, 5-10 cm. long, much shorter than the lamina, dull yellowish to reddish brown or purple-gray, glabrous, or sparsely fibrillose-scaly near the base, terete, faintly marginate adaxially; lamina linear or narrowly elliptic, glabrous, membranaceous, gradually reduced at both ends, the apex terminating in a narrow, pinnatifid apex, not proliferous; rachis glabrous, reddish brown to purplish, narrowly green-alate adaxially; pinnae very numerous, 2.5-7 cm. long, 0.7-1.4 cm. broad, sessile, narrowly adnate, approximate to subdistant, horizontally spreading, lanceolate-falcate, long-attenuate, inequilateral at base, basiscopically excavate, acroscopically truncate to subcordate, subauriculate and sometimes overlapping the rachis, the margins strongly and subacutely serrate, the teeth about 16-24 acroscopically; veins simple (or forked at the acroscopic pinna base), commonly distinct, the tips not enlarged, ending short of the margin; sori inframedial, linear to narrow-elliptic, often slightly curved, 2-6 mm. long, 0.4-0.8 mm. broad; indusium delicate, linear, yellow to brownish or hyaline, subentire.

This has been treated by various authors as a variety of *A. erectum*, a species perhaps confined (in the strict sense) to the Old World tropics. For further discussion, see *A. erectum* under "Dubious or Excluded Species."

Asplenium heterochroum Kunze, Linnaea 9: 67. 1834. *A. trichomanes* L. var. *repens* Daven. Bull. Torrey Bot. Club 13: 130. 1886. *A. muticum* Gilbert, Amer. Bot. 4: 86. 1903. *A. palmeri* Maxon, Contr. U.S. Natl. Herb. 13: 39. 1909.

In forests or shaded cliffs, on rocks (commonly limestone) or in

crevices of cliffs, or rarely on the forest floor, 150-1,600 m.; Alta Verapaz; Petén; Sololá. Southern United States; Bermuda; Greater Antilles; Mexico; British Honduras; Colombia; Venezuela; Ecuador.

Plants epipetric, rarely terrestrial; rhizome short, erect, provided at apex with linear, blackish, obscurely clathrate scales, these often with narrow, brown margins; leaves numerous, erect, densely caespitose, 6-22 cm. long and 1-1.5 cm. broad; petiole 0.3-3 cm. long, much shorter than the lamina, terete, lustrous, atropurpureous to blackish, narrow-alate often to the base (the wings frequently deciduous), glabrous or sparsely provided with dark, fibrillose scales or trichomes; lamina glabrous, simply pinnate, firm-herbaceous, linear, gradually reduced to base and terminating abruptly in a non-conform apical segment, or sometimes the apex naked and radican, provided with a proliferous bud; rachis atropurpureous to blackish, essentially glabrous, terete abaxially, somewhat flattened and narrow-alate adaxially; pinnae numerous, 4-10 mm. long and 2-4 mm. broad, commonly 2-2.5 times as long as broad, patent or slightly deflexed, subdistant or remote, never crowded or imbricate, elliptic or broadly oblong, somewhat auriculate acroscopically, sessile or minutely stalked, margins subentire to crenate, or broadly serrate; veins distinct to obscure (but usually distinct when leaves are held to light), simple (or the basal fertile ones sometimes 1-forked), not terminating in enlarged, distinct hydathodes; sori in several pairs, borne nearer the midrib than the margin (except when confluent at maturity); indusium broad, pale yellowish or whitish, entire to erose, persistent, but sometimes nearly obscured at maturity by the numerous, spreading sporangia.

This and *A. resiliens* Kunze are very closely related and may be difficult to separate, especially when leaf texture is so opaque that the forking of fertile veins cannot be seen in the latter. However, this very opacity may serve as a key character, for leaf texture of *A. heterochroum* is rarely so thick as to obscure the simple, fertile veins, at least when the leaf is held up to strong light.

There appears to be little justification in maintaining *A. palmeri* as a distinct species. It was said to differ from *A. heterochroum* because it was a somewhat smaller, thicker-textured plant, with a proliferous leaf tip. However, in most specimens I have examined which have proliferous apices, as many normal leaves may be borne on the same rhizome. Leaf texture, also, is apt to vary in this species complex, from firm-herbaceous to subcoriaceous. Such variation can easily result from the conditions occurring in different habitats where the plants are found.

Asplenium hoffmannii Hieron. Hedwigia 60: 258. 1918. *A. membranifolium* Maxon, Amer. Fern J. 24: 72. 1934.

In forests, on wet rocks, or on banks of streams, 700-1,200 m.; Retalhuleu; Santa Rosa. El Salvador; Costa Rica; Panama; Colombia.

Plants terrestrial or epipetric; rhizome short-creeping, provided (at petiole bases) with dark-brown to blackish, lanceolate, attenuate, clathrate scales, these somewhat lustrous, entire, 1-2.5 mm. long; leaves pinnate, usually 2 or 3 and crowded on the

rhizome, 10-20 cm. long, 3.5-6 cm. broad; petiole delicate, marginate or inconspicuously alate, commonly flattened and fleshy, greenish, or dull reddish brown, much shorter than the lamina, scales few (at base) or lacking; lamina broadly oblong to deltoid-ovate, membranaceous, scarcely reduced at base, gradually tapering to a pinnatifid apex, not proliferous; rachis greenish, flattened, fleshy, narrow-alate, glabrous; pinnae 5-8 pairs, 2-4 cm. long, 0.8-2 cm. broad, sessile (or basal ones minutely stalked), crowded or moderately spaced, horizontal to slightly ascending, ovate- or oblong-trapeziform, obtuse to subacute, inequilateral at base, narrow-cuneate to excavate basiscopically, truncate (and sometimes subauriculate) acroscopically, rather deeply 1- or 2-crenate or obtusely serrate, the midrib flexuous and usually not well-defined; veins simple to 1- or 2-forked, or the basal acroscopic one pinnately branched, the tips not enlarged, ending well short of the margin; sori linear, 2-5 mm. long, less than 0.5 mm. broad, straight or slightly curved, sometimes double (diplazoid), most of them nearer the midrib than the margin; indusium linear, delicate, greenish to hyaline, subentire or slightly erose.

These small ferns are represented in herbaria by few collections. The species is closely related to *A. delitescens*, from which it differs mainly in size of leaf and shape of pinnae. In more significant features, however, the two are quite similar: short-creeping rhizomes with minute dark-brown scales at petiole base, relatively few pinnae, delicate, narrow indusia, and the not uncommon occurrence of diplazoid sori.

Asplenium kellermanii Maxon, Contr. U.S. Natl. Herb. 17: 152. 1913. *A. pinnatum* Copel. Univ. Calif. Publ. Bot. 19: 289. 1941 (type from Petlacala, west of Reyes, stream bank in shade, alt. 1,810 m., Guerrero, Mexico, *Mexia* 9048).

Apparently known only from the type (Volcán Atitlan, Sololá, *Kellerman* 5792) and the type of *A. pinnatum*.

Plants terrestrial; rhizome stout, erect to ascending, provided with linear, attenuate, blackish scales, these obscurely clathrate, with the cells narrow and crowded; leaves 20-50 cm. long, 4-7 cm. broad, fasciculate, simply pinnate; petiole about as long as the lamina, lustrous, dark brown to atropurpureous, glabrous, terete, nonalate, but often with 2 minute, parallel ribs adaxially near the lamina; lamina narrowly oblong, glabrous, chartaceous to subcoriaceous, scarcely reduced at base, imparipinnate, the apical segment subconform or hastate; rachis glabrous, dark brown or atropurpureous, abaxially terete, adaxially slightly flattened and narrow-alate; pinnae 5-8 pairs, to 5 cm. long and 2 cm. broad, subopposite, remote, patent, subdeltoid, acute, broadly cuneate or truncate at base, margins entire to crenulate; veins indistinct or obscure, subflabellate, 1- to 2-forked and spreading from the midrib at a narrow angle, terminating in slightly enlarged hydathodes; sori long and narrow, 4-5 on either side of the midrib; indusium fragile, linear, whitish to pale brown, subentire.

This closely matches the description of *A. obesum* Bak., the type of which is reported from Guatemala. See discussion of the latter under "Dubious or Excluded Species."

Asplenium laetum Sw. Syn. Fil. 79: 271. 1806 (not Schkuhr, 1809 nor Wall. 1828).

In forests, on slopes, and river banks, and on rocky bluffs or wooded ravines, 50-1,100 m.; Alta Verapaz; Escuintla; Huehuetenango; (Izabal?); Petén; Sacatepéquez. West Indies; Mexico to Paraguay and Argentina; Old World.

Plants terrestrial; rhizome short-creeping, provided at the apex with dark-brown or blackish, linear scales, these clathrate (sometimes obscurely so), the cells long and narrow; leaves to 40 cm. long, 4-10 cm. broad, crowded, simply pinnate; petiole shorter than or nearly as long as the lamina, commonly lustrous, dark, reddish brown to atropurpureous (but sometimes dull and grayish or greenish brown), glabrous, but with a few, scattered, hairlike scales toward the base, abaxially terete, adaxially sulcate and often subquadrangular, nonalate; lamina oblong to lanceolate, essentially glabrous, thin-herbaceous, sparsely and minutely glandular abaxially, scarcely or not reduced at base, gradually diminishing to a narrow, pinnatifid apex; rachis essentially glabrous, greenish to grayish brown, but commonly reddish brown or atropurpureous in the proximal portion, somewhat flattened, greenish marginate or very narrow-alate distally; pinnae 10-20 pairs, to 6 cm. long and 1.5 cm. broad, subsessile or short-stalked, alternate, approximate or subdistant, spreading to slightly ascending, oblong to trapeziform, obtuse to acute, subdimidiate at base, truncate acroscopically, cuneate to excavate basiscopically, margin (at least the acroscopic one) crenate to serrate; veins mostly distinct, spreading at narrow angles from the midrib, 1- to 2-forked, ending in the teeth or crenulations short of the margin, the tips slightly enlarged; sori long and narrow, 5-10 on either side of the midrib, rarely diplazioid; indusium pale green or yellowish, fragile, linear, subentire.

Color and glossiness of the petiole is usually an effective character for delineating groups of species within the genus: most species have petioles which are either blackish to atropurpureous *and* highly lustrous, or greenish to brown *and not* (or scarcely) lustrous. However, *A. laetum* is one of a few species where this feature is not always reliable, for although the petiole is most commonly dark and shining, a number of specimens (at least in Guatemala) have been examined on which they are dull and lighter colored. Such color variance has been observed even among petioles borne on the same rhizome.

Asplenium miradorens Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 243 (*seors.* 91). 1849.

In wet forests, on shaded slopes or on banks of wooded ravines, 900-2,100 m.; Baja Verapaz; Chiquimula; Sacatepéquez; Zacapa. Southern Mexico; Honduras; Nicaragua; Costa Rica.

Plants commonly terrestrial; rhizome erect to ascending, amply provided with lanceolate to linear, rigid, reddish brown scales, these 2-3 mm. long, obscurely clathrate, short-attenuate (but not filiform-tipped); leaves pinnate, subcaespitose, mature ones 20-40 cm. long, 4-5 cm. broad; petiole stout, 4-10 cm. long, much shorter than the lamina, gray-green or dull yellowish to reddish brown, terete to somewhat flattened, marginate or very narrowly alate toward the apex, sparsely scaly at the base, the scales like those of the rhizome, but 4-5 mm. long and more obviously clathrate; lamina linear or narrowly elliptic, thin- to firm-membranaceous, gradually reduced at both ends, the apex gradu-

ally terminating in a pinnatifid or serrate apex, not proliferous; rachis glabrous, greenish or yellowish to reddish brown, narrow-alate throughout; pinnae 20-35 pairs, middle ones 2-3 cm. long, 0.7-1.5 cm. broad, sessile to short-stalked, approximate to crowded, horizontally spreading, oblong to lanceolate, obtuse to subacute, inequilateral at base, basiscopically cuneate or excavate, acroscopically truncate and often subauriculate, not (or only rarely) overlapping the rachis, the margins obtusely or subacutely serrate to biserrate; veins distinct, those of the acroscopic side mostly 1-forked, the basal one 2-forked, the distal ones and those of the basiscopic side simple, the tips not enlarged, ending well short of the margin; sori mostly medial, linear to elliptic, relatively short, 1.5-3 mm. long and 0.3-0.8 mm. broad; indusium delicate, linear, pale yellowish or hyaline, subentire.

With this should probably be included *A. standleyi* Maxon of El Salvador, which was said by Maxon to differ slightly in color, texture, depth of serrations, and shorter sori. Guatemalan specimens of *A. miradorensis* appear to be darker colored, more robust plants, with more obtuse pinnae; but when collections throughout the entire range are more carefully compared, it is likely none of these features will be significant or consistent.

For a further comparison of this with other species, see treatment of *A. williamsii*; also see *A. erectum*, under "Dubious or Excluded Species."

Asplenium monanthes L. Mantissa Pl. 130. 1767. *A. monanthemum* L. Syst. Veg. ed. 14: 933. 1784. *nom. illeg.* *A. polyphyllum* Bertol. Novi Comment. Acad. Sci. Inst. Bononiensis 4: 443. 1840 (type from Volcán de Agua, Guatemala, *Bertoloni s.n.*) (not Presl ex Goldm. 1843). *A. arcuatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. I: 241 (*seors.* 89). 1849. *A. polymeris* Moore, Index Fil. 154. 1857 (erroneous renaming of *A. polyphyllum*). *A. bertolonii* Donn.-Sm. Enum. Pl. Guat. 4: 189. 1895 (erroneous renaming of *A. polyphyllum*).

An ubiquitous fern, growing in various habitats, in forests (or rarely in open areas), most commonly in ravines or on slopes of volcanoes, on shaded banks, on rocks or in rock crevices, or on tree trunks, 1,000-3,300 m.; Alta Verapaz; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Jutiapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Santa Rosa; Suchitepéquez; Totonicapán; Zacapa. United States (Arizona); Mexico; El Salvador to Panama; Jamaica; Hispaniola; Colombia; Venezuela; Ecuador; Peru; Bolivia; Brazil; Argentina; Hawaii; Africa.

Plants terrestrial, epipetric, or epiphytic; rhizome short, stout, amply provided with linear (or rarely ovate), dark-brown to blackish scales, these often faintly bicolorous (with narrow, lighter brown margins), opaque, obscurely clathrate, the cells mostly narrow (especially near the margin), the cell walls thick; leaves numerous, erect or

sometimes pendent, densely caespitose, to 65 cm. long and 3 (3.5) cm. broad; petiole 1-20 cm. long, much shorter than the lamina, terete (but appearing slightly flattened adaxially due to the presence of 2 minute, parallel ribs), lustrous, commonly atropurpureous (rarely dark brown or blackish), nonalate, sparsely provided with dark, fibrillose scales; lamina glabrous, simply pinnate, firm-herbaceous to chartaceous, linear, gradually reduced to base, and diminished to a pinnatifid, sometimes caudate, apex; rachis terete, commonly atropurpureous, sparsely provided with dark, fibrillose scales, sometimes proliferous at or near the apex, provided adaxially with thin, cartilaginous ribs which commonly become perpendicular wings distally; pinnae numerous, 5-16 mm. long, 2-5 mm. broad, (2) 2.5-5 times as long as broad, patent, blunt and quadrangular to acute and subfalcate, dimidiate, subsessile, sometimes appearing nodose-articulate, the cuneate green base often arising from a circular depression on the rachis, margins subentire, or the acroscopic margin crenulate; veins obscure or indistinct, terminating short of the margin in enlarged hydathodes, which are conspicuous adaxially; sori solitary near the basiscopic margin, or borne in several pairs, these often confluent at maturity; indusium relatively large and broad, pale green to whitish, subentire, persistent, but often obscured at maturity by the numerous, spreading sporangia.

Very closely related to *A. castaneum*, under which see further discussion.

***Asplenium myriophyllum* (Sw.) Presl, Rel. Haenk. 1: 48. 1825.**
Caenopteris myriophylla Sw. J. Bot. (Schrader) 1800 (2): 60. 1801.
Darea myriophylla Willd. Sp. Pl. 5: 301. 1810.

In forests, on the forest floor or (in Guatemala) commonly on rocks or in crevices of limestone cliffs, 900-1,600 m.; Alta Verapaz. Mexico; Honduras; Costa Rica; Panama; West Indies; Colombia; Venezuela; Ecuador; Peru.

Plants terrestrial or (in Guatemala) commonly epipetric; rhizome erect, provided at apex with a small number of minute, dark-brown scales, these ovate to lanceolate, 0.1-1.2 mm. long, obscurely clathrate, the lamina isodiametric or somewhat elongated, and with thick walls; leaves (throughout the range) to 50 cm. long and 12 cm. broad, but in ours rarely over 11 cm. long and 2 cm. broad, 2-pinnate (in ours) to nearly 3-pinnate, fasciculate; petiole 0.2-2 cm. (in ours) to 20 cm. long, 0.2-1 mm. in diameter, reddish or grayish brown, not or slightly lustrous, narrow-marginate, with scales lacking or a few, minute, ovate ones scattered near the base; lamina glabrous, thin- to firm-herbaceous, bright green, oblong or lanceolate-elliptic, (1.5) 2-6 times as long as the petiole, gradually reduced to a minute but subconform apex and strongly and gradually reduced at base; rachis reddish or greenish brown, marginate to narrowly alate; pinnae 8-24 pairs, median ones 1 cm. (in ours) to 6 cm. long, approximate to crowded, ascending, or some proximal ones deflexed, sessile or subsessile, the basal acroscopic pinnules commonly overlapping the rachis; costae greenish brown to blackish, commonly alate; pinnules stalked (at least the proximal ones), 1-4 (in ours) to 12 pairs, simple, bifid, or subdigitately lobed (in ours) to pinnate; ultimate segments oblong to obovate; veins simple in each of the ultimate segments, commonly distinct, sometimes blackish; sori 1 to a segment, short and relatively broad, often filling the space between the vein and the acroscopic margin; indusium broad, entire, delicate, whitish or scarious.

Asplenium myriophyllum in Guatemala at first appears to be dif-

ferent from the species as it occurs elsewhere in the range. In all available collections examined, the leaves, though completely fertile, are not more than 11 cm. long and 2 cm. broad and are rarely more than bipinnate. Many of these specimens have been determined in herbaria as *A. divaricatum* Kunze, a Peruvian fern very similar in size and dissection of leaf. However, the lamina of the latter is fleshier and opaque, the rhizome scales are linear, often with narrow, brown margins, and the petiole scales are more numerous, tortuous, and single-ribbed.

Most specimens of typical *A. myriophyllum* are coarser, and many times larger than the Guatemalan plants, and except for reduced lamina base and short petioles, are scarcely distinguishable from *A. cristatum* (under which see further discussion). The question arises as to whether our plants are merely precociously fertile juveniles, but since they are relatively numerous in the collections, and so consistent in their features, I believe it may be more likely that they, along with a scattering of similarly reduced ferns from Central America and the West Indies, may constitute a new variety. (In some early notes concerning the genus in Guatemala, C. V. Morton was apparently considering this to be a new species, "*A. isomerum*.") However, this and the entire species complex, including *A. cristatum*, *A. dentatum*, and *A. myriophyllum*, need careful study in the herbarium and field before the taxonomy is fully understood. Thus I feel it is unwise to create a new species or variety at this time.

Asplenium olivaceum A. R. Smith, Proc. Calif. Acad. Sci. 40: 212. 1975.

Known from the type: summit of Cerro Sillab, Senahú, limestone cliffs, 6,000 ft., Alta Verapaz, *Hatch & Wilson 149*, and one other: limestone rocks, along Comitán River, 1,300 m., La Trinitaria, Chiapas, Mexico, *Breedlove & Smith 22379* (in part).

Plants epipetric; rhizome short, erect, provided at the apex with linear, blackish, obscurely clathrate scales, these often with attenuate apices; leaves several, crowded, erect or arching, 6-12 cm. long, about 1.5 cm. broad; petiole 2-4 cm. long, terete, lustrous, blackish, narrow-alate often to base (the wings often deciduous), glabrous or sparsely provided with dark, fibrillose scales or trichomes; lamina glabrous, simply pinnate, thin-herbaceous, narrow-oblong, scarcely or not at all reduced at base, terminating abruptly in a nonconform apical segment, not proliferous; rachis blackish, essentially glabrous, abaxially terete, adaxially somewhat flattened and alate; pinnae 8-15 pairs, 5-8 mm. long, 3-5 mm. broad, some of them nearly as broad as long, patent, subdistant to somewhat crowded, broadly oblong, slightly or not at all auriculate, sessile, margins entire to slightly undulate-crenate; veins distinct or indistinct, but quite distinct when leaves are held to light, at least the fertile ones simple, not terminating in enlarged, distinct hydathodes; sori solitary, borne near and parallel to the inferior mar-

gin, or rarely another one borne on the basal acroscopic vein; indusium broad, whitish to light gray, subentire, persistent.

Asplenium praemorsum Sw. Prodr. Veg. Ind. Occ. 130. 1788.

In forests, on tree trunks or fallen logs, on rocks, or occasionally on banks of ravines or rivers, 750-3,000 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez. West Indies; Honduras and El Salvador to Colombia and Venezuela, south to Brazil and Bolivia; Argentina.

Plants epiphytic or epipetric, rarely terrestrial; rhizome erect, stout, densely provided with linear, attenuate scales, these lustrous, dark brown to black, often faintly bicolorous, with very narrow, lighter brown margins; leaves to 60 cm. long and 9 cm. broad, nearly 2-pinnate, rigid, crowded to caespitose; petiole equaling or shorter than the lamina, terete abaxially, sulcate adaxially, dark brown to blackish, amply to abundantly scaly, the scales dark brown to blackish, filiform, single-ribbed, from a broadened, clathrate base; lamina subcoriaceous, lanceolate or narrow-ovate, tapering to a pinnatifid apex, slightly or not at all reduced at base, abundantly filiform-scaly on the abaxial side; rachis scaly, terete and dark brown or black abaxially, sulcate and greenish adaxially, not proliferous; pinnae (in ours) 6-15 pairs, to 5 cm. long, spreading to slightly ascending, short-stalked, inequilateral at base, cut nearly or quite to the ill-defined costa into several pairs of elongated, often obovate or flabelliform segments, these subentire to dentate or lacerate; sori borne on the veins adjacent to the segment midrib at a very narrow angle, appearing subparallel to the midrib and to the segment margins; indusium drying brownish or yellow, elongated, narrow.

In the Morton and Lellinger treatment of the Venezuelan *Aspleniums* (1966), it is pointed out that *A. praemorsum* in Venezuela is "apparently always saxicolous." However, the habitat of the species is far less restricted in Guatemala, for these ferns have been reported growing on tree trunks, fallen logs, rocks and crevices of cliffs, ravine banks, and in the moist earth of river banks. It is interesting to note that *Standley* 86168 and 86169 (presumably collected near each other on Cerro Quemado, Quezaltenango, alt. 2,900-3,000 m.) were found in different habitats. Both are fully mature ferns, the first collected "on rock," a diminutive plant only 15 cm. tall, with small, one- or two-lobed pinnae. The second, found "on tree," has leaves over 50 cm. long, with large, many-lobed pinnae, and many of the lobes in turn deeply lacerate.

Specimens of *A. praemorsum* have been identified in various herbaria as *A. aethiopicum* (Burm.) Becherer (*A. furcatum* Thunb.), but as Morton & Lellinger (1966) have shown, our plants are distinct from this Old World species in a number of characteristics.

Asplenium pteropus Kaulf. Enum. Fil. 170. 1824. *A. lunulatum* Sw. var. *pteropus* (Kaulf.) Sodiro, Anales Univ. Quito 8: 276. 1893. *A. pseudirectum* Hieron. Hedwigia 60: 239. 1918.



FIG. 11. *Asplenium* (decompound species). a, *A. rutaceum*, habit, $\times \frac{1}{2}$; b, *A. cuspidatum* var. *tenerrimum*, habit, full size; c, *A. cristatum*, pinna, $\times \frac{1}{2}$, and pinna base, $\times 3$; d, *A. achilleifolium*, pinna, $\times \frac{1}{2}$, and pinna section, $\times 3$; e, *A. commutatum*, rachis scale, $\times 25$; f, *A. praemorsum*, rachis scale, $\times 25$; g, *A. cuneatum*, scale from petiole base.

In dense, wet forests or forested ravines, commonly on trunks and lower branches of trees, but sometimes on wet ravine banks or on mossy rocks, sea level to 2,600 m.; Alta Verapaz; Huehuetenango; Izabal; Quezaltenango; San Marcos; Suchitepéquez. West Indies; southern Mexico to Panama; Colombia to British Guiana, south to Bolivia and Brazil.

Plants commonly epiphytic, sometimes terrestrial or epipetric; rhizome erect to ascending, amply provided with lanceolate or linear-lanceolate, castaneous to dark-brown, clathrate scales, these 3-5 mm. long, often attenuate (but not filiform-tipped); leaves pinnate, crowded to subcaespitose, mature ones (in Guatemala) 10-40 cm. long, 2-8 cm. broad; petiole wiry to stout, 1-8 cm. long, much shorter than the lamina, gray to green or dull reddish brown, glabrous or sparsely scaly at the very base, terete to somewhat flattened, broadly alate toward the lamina or throughout, each of the wings commonly 0.4-1 mm. broad; lamina linear or narrowly elliptic, glabrous, thin- to firm-membranaceous, gradually reduced at both ends, the apex gradually terminating in a pinnatifid or serrate apex, not (or very rarely) proliferous; rachis glabrous, dull greenish or yellowish to reddish brown, green-alate throughout; pinnae 16-30 pairs, middle ones 1-4 (5) cm. long, 0.4-1.2 cm. broad, sessile, approximate, horizontally spreading, oblong to lanceolate, obtuse, or acute to acuminate, rarely (if ever) long-attenuate, inequilateral at base, basiscopically cuneate to excavate, acroscopically truncate and often subauriculate, the margins obtusely to subacutely crenate or serrate (or subentire basiscopically), the teeth commonly 7-12 acroscopically, 2-8 basiscopically; veins simple (or forked at the acroscopic base), commonly distinct, the tips not enlarged, ending well short of the margin; sori medial to inframedial, linear and slightly curved to elliptic and straight, 1.5-4 mm. long, 0.3-1 mm. broad; indusium delicate, linear, pale yellowish to hyaline, subentire.

Hieronymous (1918) described his *A. pseudirectum* as differing from *A. pteropus* in the more narrowly winged petioles and in the narrower, smaller, more crowded and numerous pinnae. In a variable and widespread species such as *A. pteropus*, these are hardly valid features on which to base a new species. I examined groups of Guatemalan and West Indian specimens which at first appeared to differ even more substantially from *A. pteropus* than in Hieronymous's description. These have narrow-alate petioles only 0.5-1 cm. long, and obtuse, subdimidiate pinnae 1-1.5 cm. long. Contrasted with "typical" specimens of *A. pteropus*, which have broadly alate petioles 3-8 cm. long, and acute, more equilateral pinnae, these plants would seem to constitute another species, or at least a good variety. However, among dozens of plants I examined throughout the entire range of *A. pteropus*, these characters vary so widely and blend so insensibly that there appears to be no point(s) at which one can designate a separation of taxa.

Asplenium pteropus belongs to a rather large species complex, associated with the Old World *A. erectum*. Further discussion may be found under the latter, in "Dubious or Excluded Species."

Asplenium pumilum Sw. Nov. Gen. & Sp. Pl. Prodr. 129. 1788. *A. minimum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 55, t. 15, f. 1. 1842 (type from Chinantlá, Oaxaca, Mexico, *Galeotti 6286*). *Athyrium verapax* Christ, Bull. Herb. Boissier II. 6: 292. 1906 (type from Cubilguitz, Alta Verapaz, Guatemala, *Tuerckheim* [ed. Donn.-Sm. 8818]) (not *Asplenium verapax* Donn.-Sm. 1888). *Athyrium leucothrix* Maxon, Proc. Biol. Soc. Wash. 43: 85. 1930 (*nom. nov.* for *Athyrium verapax* Christ).

On limestone rocks, fallen logs, or on the forest floor, in thickets or wooded ravines in wet forests, 300-1,600 m.; Alta Verapaz; Chiquimula; Huehuetenango; Petén; Santa Rosa; Sololá. Florida; West Indies; Mexico; Honduras; Nicaragua to Colombia and Venezuela, south to Peru and Brazil; Africa.

Plants terrestrial or epipetric; rhizome small, erect, provided at apex with linear, gray-brown to blackish scales, these to 3 mm. long, with attenuate, single-ribbed tips; leaves pinnate to pinnate-pinnatisect, subcaespitose, mature ones 5-25 cm. long, 1.5-10 cm. broad; petiole delicate, 1.5-14 cm. long, often as long as or longer than the lamina, green, or often lustrous and castaneous to atropurpureous at base (on the abaxial side), terete abaxially, green-marginate and flattened or shallowly sulcate adaxially, glabrous, or more often amply to densely provided with white, septate trichomes, as well as with scattered blackish, hairlike scales; lamina ovate to subdeltoid, tissue glabrous or the axes, veins, and margins septate-hirsute, firm-herbaceous to somewhat fleshy, opaque, not reduced at base, terminating in a nonconform, pinnatifid apex, not proliferous; rachis greenish, marginate to narrowly alate toward the base, more broadly so above; pinnae 1-5 pairs, 1-6 cm. long, sessile and adnate distally, the proximal ones often short-stalked, approximate to subdistant, slightly ascending, most of them lanceolate, obtuse to somewhat attenuate, subentire to crenate, bicrenate or lobed, basal pair much the largest, strongly produced basiscopically, the proximal pair of lobes often cut nearly to the costa; veins 1- or 2-forked, or pinnately branched in the basal lobes, distinct or indistinct, the tips not enlarged, ending short of the margin; sori linear to elliptic, commonly straight and lying at a narrow angle (often subparallel) to the segment midrib; indusium delicate, yellow to whitish, subentire to erose, sometimes ciliate.

Most species of *Asplenium* have pinna bases more strongly produced on their acroscopic side, with the basiscopical side narrowly cuneate or conspicuously excavate, or in a smaller number of species the pinna bases are subequilateral. However, *A. pumilum* is one of a few species in the genus in which the basal pinnae have their basiscopical lobes much more strongly produced—usually 2-4 times larger than the opposing acroscopic ones. Other distinctive features are pubescence and petiole color. The petiole is commonly green, except that it becomes dark and shiny abaxially, especially toward the base. The axes, veins, and margins are typically provided with white, septate trichomes. Often the pubescence is dense and conspicuous; sometimes only the margins are minutely hirsute; rarely the leaf is glabrous.

Other species of *Asplenium* in Guatemala may be variously provided with scales, these often hairlike and dark, but seldom with true trichomes, and then not white or septate.

Earlier workers have separated *A. minimum* from *A. pumilum* on the basis of the former's smaller size and glabrous leaves, and *A. leucothrix* and *A. verapax* because of their more abundant pubescence or deeper cutting. However, a study of large numbers of collections throughout the range indicates that size, dissection, and pubescence are much too variable to be significant.

Asplenium radicans L. Syst. Nat. ed. 10, 2: 1323. 1759 (not Schkuhr, 1809, Pritch. 1836, nor Bak. 1867).

Plants terrestrial (rarely epipetric); rhizome stout, erect, amply provided at apex with linear or lanceolate, gray-brown, subclathrate scales; leaves to 60 cm. long and 25 cm. broad, pinnate to 3-pinnate-pinnatifid, fasciculate; petiole to 10 cm. long, terete, or sulcate adaxially, dark brown to atropurpureous, lustrous, nonalate, essentially glabrous; lamina thin- to firm-herbaceous, lanceolate to ovate, scarcely reduced at base, gradually and strongly tapering to the apex, ostensibly glabrous but sparsely provided abaxially with appressed, very minute, glandular trichomes; rachis dark brown to atropurpureous, shallowly sulcate and marginate or narrow alate adaxially, naked and flagelliform at the apex of the lamina, with a proliferous tip; pinnae numerous, highly variable, simple, serrate, and 2-3 cm. long by 1 cm. broad in var. *cirrhatum*, to 2-pinnate-pinnatifid and often 12-16 cm. long by 4-5 cm. broad in var. *uniseriale*, patent to slightly ascending, sessile or subsessile, the basal pinnules of highly dissected varieties overlapping the rachis; veins commonly 1- or 2-forked, or simple in the ultimate segments of decompound varieties; sori elongated, but less so in decompound varieties; indusium thin, yellowish or greenish, oblong to elliptic, subentire.

There are few species of ferns which can match this one in variability of leaf dissection. Dozens of species and varieties have been described through the years, based solely on the shape and cutting of pinnae, with the result that the taxonomy of the species complex has become nearly chaotic. With its shining, dark-purple petioles and flagelliform, radicant leaf tips, it is rather easily distinguished from most other species of *Asplenium*, and its two extremes (the simply pinnate vs. the tripinnate lamina) would seem to represent distinct species. However, between these extremes appear to exist every possible degree of leaf dissection, each one of which merges insensibly with adjacent ones. Furthermore, many of these may be found scattered liberally throughout the range. A detailed analysis of the aggregate species is sorely needed, but until such a study has been completed, there is little recourse but to maintain a number of varieties, using rather arbitrary limits. Four (possibly five) such varieties are suggested in Guatemala.

Asplenium radicans var. *cirrhatum* (L. C. Rich.) Rosenst. Hed-

wigia 46: 102. 1906. *A. cirrhatum* L. C. Rich. ex Willd. in L. Sp. Pl. ed. 4, 5: 321. 1810.

Terrestrial, in wet forests, 350-1,000 m.; Alta Verapaz. West Indies; Honduras; Nicaragua to Colombia and Venezuela, south to Bolivia and Brazil.

Lamina simply pinnate; pinnae (in ours) 2-4 cm. long and 0.8-1.2 cm. broad, subentire to broadly and bluntly serrate, obtuse or subacute, sessile to subsessile, narrowly cuneate at the basiscopic base, broadly cuneate to truncate and scarcely or not at all auriculate acroscopically.

***Asplenium radicans* var. *partitum* (Kl.) Hieron.** Bot. Jahrb. Syst. 34: 464. 1904. *A. flabellulatum* var. *partitum* Kl. Linnaea 20: 357. 1847. *A. partitum* (Kl.) C. Chr. Index Fil. 125. 1905.

On forest floor or in wooded ravines, 1,100-1,800 m.; Alta Verapaz; Chimaltenango. West Indies; Mexico; Honduras; Nicaragua to Peru and Bolivia.

Lamina pinnate-pinnatifid to fully 2-pinnate; pinnae 2.5-8 cm. long and 1-2.2 cm. broad, pinnate at least in the proximal half, obtuse to acute, sessile to short-stalked, at base cuneate basiscopically, truncate acroscopically; secondary segments (or pinnules) 5-10 pairs, adnate to short-stalked, obovate or broadly oblong, obtuse, subentire to coarsely toothed, or (rarely) acroscopically lobed.

This differs from var. *radicans* in that several to most pairs of segments on each pinna are narrowed to short but definite stalks, and most segments are coarsely toothed at the apex, or occasionally even deeply lobed. In var. *radicans*, pinnae may be cut (especially in their proximal half) nearly to the alate costa, but the segments are adnate to the rather broad wing, and their margins are rarely toothed.

***Asplenium radicans* var. *radicans*.** *A. rhizophyllum* L. Sp. Pl. ed. 2: 1540. 1763 (not *A. rhizophyllum* L. 1753). *A. rhizophorum* L. Gen. Pl. ed. 6 *emend.* 1764. *nom. illeg.* *A. alloeopteron* Kunze ex Kl. Linnaea 20: 353. 1847. *A. cyrtopteron* Kunze, *op. cit.* 23: 233. 1850.

Terrestrial, in wet forests, 1,500-2,200 m.; Alta Verapaz; Baja Verapaz; El Progreso. West Indies; Southern Mexico; Honduras to Brazil and Bolivia.

Lamina pinnate-pinnatifid to nearly 2-pinnate; pinnae 3-10 cm. long, 0.8-3 cm. broad, most of them deeply lobed, often nearly to the broadly alate costa, acute to acuminate, sessile or subsessile, the base commonly irregular, truncate acroscopically, cuneate basiscopically; secondary segments mostly elongated, lanceolate to narrow-ovate or obovate, obtuse to subacute, broadly or narrowly adnate to the costal wing, margins subentire or vary rarely coarsely and bluntly toothed.

This and var. *partitum* are sometimes easily confused, and further

comparisons are made under discussion of the latter. *Asplenium alloeopterum* has been suggested as an intermediate between the two, but such splitting of *A. radicans* into further intermediate varieties can serve no useful purpose and, in fact, must eventually result in the establishment of literally dozens of more varieties, few of which will be discrete.

Asplenium radicans var. **uniseriale** (Raddi) Gómez, Brenesia 8: 53. 1976. *A. uniseriale* Raddi, Opusc. Sci. 3: 291. 1819. *A. rachirrhizon* Raddi, Pl. Bras. 1: 39, t. 56. 1825. (*A. flabellulatum* Kunze, Linnaea 9: 71. 1834?). *A. amabile* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 251 (seors. 99). 1849.

On the forest floor or in wooded ravines, occasionally found on rocks or on the rocky banks of ravines, 50-800 m.; Huehuetenango; Izabal; Quezaltenango. West Indies; Southern Mexico; Honduras to Colombia and Venezuela, south to Brazil and Bolivia.

Lamina 2-pinnate-pinnatifid to 3-pinnate, thin-herbaceous; pinnae 7-16 cm. long, 2-5 cm. broad, oblong to narrow-ovate, acute to acuminate or in larger leaves often attenuate and the tips proliferous, sessile, the basal pinnules crowding or often overlapping the rachis; pinnules 8-18 pairs, short-stalked, again pinnate, with 2-4 pairs of segments; tertiary segments 1-3 pairs, often only 2 mm. long and 1 mm. broad, adnate or stalked, commonly obovate or cuneiform, simple to bifid (or on larger leaves occasionally subflabellate), with margins entire.

Of all the varieties occurring in Guatemala, this is the easiest to distinguish because of its greatly dissected lamina and minute ultimate segments. However, it is itself extremely variable, and the larger forms might possibly invite further varietal separation. The typical habit (most common in Guatemala and Brazil) is one of smaller laminae and more delicate segments, with leaves generally 38-50 (60) cm. long and 10-16 (17) cm. broad. The pinnae rarely exceed 10 cm. in length and commonly terminate rather abruptly in an acute or acuminate apex. The tertiary segments are mostly minute (about 2 mm. long and 1 mm. broad) and are simple to irregularly bifid. But there appears to be a form amply represented throughout the range which has leaves 50-100 cm. long and 16-28 cm. broad, with pinnae 8-18 cm. long which very gradually diminish to a subcaudate, proliferous apex. Tertiary segments on this form are much larger and are bifid to subflabellate (occasionally even pinnatifid). This larger form might correspond to Kunze's *A. flabellulatum* from Peru, or even more closely to var. *tripinnata* described by Hieronymous from Colombia. A close study of specimens collected throughout the range would be necessary to ascertain if this form really merits a varietal distinction.

Asplenium repandulum Kunze, Linnaea 9: 65. 1834. *A. riparium* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 244 (seors. 92). 1849. *A. obtusifolium* L. var. *riparium* (Liebm.) Domin, Pterid. Dominica, 175. 1929.

In dense, wet forests, on the forest floor, on shaded slopes, or in ravines, occasionally on rocks, rarely on tree trunks, 900-2,500 m.; Alta Verapaz; Baja Verapaz; Izabal; Quezaltenango; San Marcos. West Indies; southern Mexico; Nicaragua; Costa Rica; Colombia and Venezuela to Brazil and Bolivia.

Plants epiphytic, but more commonly (at least in Guatemala) terrestrial; rhizome creeping, with golden-tomentose roots and sparsely provided with inconspicuous, lanceolate or ovate scales, these dark brown, usually lustrous, entire, ca. 1 mm. long; leaves pinnate, approximate to subdistant, 25-60 cm. long, 10-18 cm. broad; petiole stout, fleshy, 2-5 mm. thick, shorter than the lamina, dull reddish or greenish brown, flattened, shallow-sulcate adaxially, glabrous, rarely with a few dark-brown lanceolate scales at base; lamina oblong to ovate, glabrous, thin-herbaceous, not or scarcely reduced at base, terminating in a subconform apical segment (i.e., much like the distal pinnae, but commonly with a broad, basal lobe), not proliferous; rachis glabrous, greenish or reddish brown, not alate (but sometimes appearing so because of its flattened and fleshy nature); pinnae 9-14 pairs, 3-11 cm. long, 1-2.5 cm. broad, sessile (or proximal ones short-stalked), widely spaced, horizontally spreading or ascending, lanceolate, acute to attenuate (rarely obtuse), inequilateral at base, narrowly cuneate to excavate basiscopically, truncate and more strongly produced (often auriculate) acroscopically, crenate to serrate; veins 1- or 2-forked, commonly distinct, the tips not enlarged, ending at or near the pinna margin; sori inframedial to nearly medial, linear, 5-10 mm. long, 0.5-1.0 mm. broad, commonly curved; indusium linear, opaque, greenish or brown, subentire.

This is very similar to *A. obtusifolium* L., of the West Indies and South America, from which it differs in the more numerous, more acute, unlobed pinnae. Pinnae of *A. obtusifolium* have a single, basal lobe which is cut nearly to the costa.

Asplenium resiliens Kunze, Linnaea 18: 331. 1844. *A. parvulum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 60, t. 15, f. 3. 1842 (type from Capulalpan and Hacienda del Carmen, Oaxaca, Mexico, Galeotti 6462) (not Hook. 1840). *A. trichomanoides sensu* Kunze, Amer. J. Sci. II. 6: 85. 1848 (not Michx. 1803).

In open forests, commonly on mountain slopes, on rocks, or in rock crevices, 1,800-3,900 m.; Huehuetenango; El Quiché; Sololá. Southern United States; West Indies; Mexico; Colombia and Venezuela to Argentina and Brazil.

Plants epipetric; rhizome short, erect, provided at apex with linear, blackish, obscurely clathrate scales, these often with attenuate apices and narrow, brown margins; leaves numerous, erect, densely caespitose, 4-20 cm. long and 0.5-1.5 cm. broad (in Guatemala); petiole 0.3-4 cm. long, much shorter than the lamina, terete, lustrous,

atropurpureous to blackish, scarcely or not at all alate, glabrous or sparsely provided with dark, fibrillose scales or trichomes; lamina glabrous, simply pinnate, subcoriaceous, linear, gradually reduced to base and diminished abruptly to a pinnatifid apex (but the latter often readily deciduous, thus the tip of the rachis naked); rachis terete, dark brown, atropurpureous, or blackish, essentially glabrous, provided adaxially with thin, parallel cartilaginous ribs or these becoming very narrow wings distally; pinnae numerous, 1.5-8 mm. long and 1-3 mm. broad (in ours), 1.5-2.5 times as long as broad, patent or slightly deflexed, discrete or (in ours) more commonly imbricate, elliptic or broadly oblong, somewhat auriculate acroscopically, sessile or minutely stalked, margins entire to crenulate; veins obscure or indistinct (even when leaves are held to light), the fertile ones 1-forked, not terminating in enlarged, distinct hydathodes; sori in several pairs, mostly crowding the margins, usually confluent at maturity; indusium broad, pale yellowish or whitish, entire to erose, persistent, but commonly obscured at maturity by the numerous, spreading sporangia.

A number of Guatemalan specimens (as well as a few examined from Peru) appear to have smaller leaves and smaller and more crowded pinnae than typical *A. resiliens* found in Mexico and the Greater Antilles. Leaves of such Guatemalan plants are frequently only 4-10 cm. long and much less than 1 cm. broad. Pinnae often measure only a few millimeters in length, are mostly imbricate, and the sori are confluent. Mexican plants are typically 20-30 cm. long and 1.5-2 cm. broad, with pinnae subdistant and sori mostly discrete. However, these stunted Guatemalan ferns presumably are nothing more than altitudinal variants, for they are consistently found at 3,000-4,000 m. and in all other features they agree with typical *A. resiliens*. Consequently there has been no attempt to assign them varietal distinction.

This species and *A. heterochroum* Kunze are very difficult to separate, especially in plants with tissue so opaque that veins are obscure. For further discussion, see treatment of the latter species.

Asplenium rutaceum (Willd.) Mett. Abh. Senckenberg Naturf. Ges. 3: 173. 1858. *Aspidium rutaceum* Willd. in L. Sp. Pl. ed. 4, 5: 266. 1810. *Asplenium conquisitum* Underw. & Maxon ex Christ, Bull. Herb. Boissier II. 7: 270. 1907.

In wet forests or wooded ravines, on tree trunks and stumps, or occasionally on mossy rocks or in rock crevices, 900-1,800 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Greater Antilles; Southern Mexico; Nicaragua; Costa Rica; Venezuela and the Guianas; Colombia to Bolivia.

Plants commonly epiphytic, but occasionally terrestrial or epipetric; rhizome stout, erect, amply provided with linear to lanceolate, castaneous or gray-brown, clathrate scales; leaves to 45 cm. long and 10 cm. broad, nearly 3-pinnate, rigid, fasciculate; petiole 1-2 (3) cm. long, terete, atropurpureous, lustrous, nonalate, essentially glabrous; lamina thin-herbaceous, dark green, lanceolate, strongly and gradually reduced to both apex

and base, ostensibly glabrous, but sparsely provided abaxially with appressed, very minute trichomes; rachis dark brown or atropurpureous, shallowly sulcate and narrowly green-alate adaxially, naked and flagelliform at the apex of the lamina, with a proliferous tip; pinnae numerous, median ones to 5 cm. long and 1.5 cm. broad (but apical and basal ones greatly reduced), patent to slightly ascending or the proximal ones deflexed, oblong, sessile, the basal pinnules commonly overlapping the rachis; pinnules 6-10 pairs, cut deeply or almost to the costa into several pairs of spatulate or obovate segments, these entire, cuneate at base; veins simple (rarely 1-forked) in each segment, the scarcely enlarged tips terminating well short of the margin; sori solitary on the vein of each segment, 1.5-2 times as long as broad; indusium delicate, yellowish or greenish, oblong to elliptic, subentire.

Asplenium serra Langsd. & Fisch., Icon. Fil. 16, t. 19. 1810. *A. progrediens* Fée, Mém. Fam. Foug. 8: 81. 1857.

In wet forests, often on wooded slopes, on tree trunks or rarely terrestrial, 400-2,900 m.; Alta Verapaz; Huehuetenango; Jalapa; El Progreso; Quezaltenango; El Quiché. Mexico to Panama; West Indies; Colombia and Venezuela, south to Bolivia and Argentina; Old World.

Plants epiphytic, rarely terrestrial; rhizome creeping, stout, in ours up to 1.5 cm. thick, densely covered with linear-lanceolate, attenuate scales, these lustrous, dark brown or blackish, clathrate, the cells nearly isodiametric; leaves to 1 m. long and 30 cm. broad, subdistant to remote, simply pinnate; petiole somewhat shorter than the lamina, dark brown to atropurpureous, densely scaly at base, sparsely so above, terete or slightly flattened, sulcate adaxially; lamina oblong-lanceolate, imparipinnate, with a conform or subconform terminal segment, firm-herbaceous to chartaceous, not or scarcely reduced at base; rachis dark brown to atropurpureous, sparsely clathrate-scaly, not proliferous; pinnae stalked, numerous, spreading to ascending, lanceolate, long-attenuate, with a cuneate or obtuse, often inequilateral base, frequently excavate basiscopically, strongly produced acroscopically, the margin serrate or irregularly biserrate, the apical "pinna" larger than 5 or 6 of the distal, lateral pairs; veins 2- to 3-forked, ascending from the costa at a very acute angle; sori borne on the veins at a very acute angle (and often appearing subparallel) to the costa, sometimes nearly confluent at maturity; indusium yellowish or brown, long and narrow, often hidden by the numerous, spreading sporangia at maturity.

Asplenium serratum L. Sp. Pl. 1079. 1753. *A. nidus* Raddi, Opusc. Sci. 3: 290. 1819 (not L. 1753).

On branches or trunks of trees, or sometimes on fallen logs, in forest or thickets or wooded ravines, sea level to 800 m.; Huehuetenango; Izabal; Petén. Southern Florida; West Indies; Southern Mexico to Argentina.

Plants epiphytic; rhizome erect, stout, densely provided at apex with dark, gray-brown to blackish, clathrate, linear or linear-lanceolate, attenuate scales, and thickly covered as well with brown, tomentose roots; leaves simple, unlobed, erect, densely caespitose, sessile or nearly so; lamina (in ours) to 70 cm. long and 8 cm. broad, dark green adaxially, lighter green abaxially, chartaceous, linear-oblancoolate, short-acuminate at apex, attenuate at base, the margin often cartilaginous, subentire, or

crenulate to bluntly serrate, glabrous, but sometimes with a few dark-brown scales scattered along the base of the midrib adaxially; veins simple or 1-forked, crowded, rather obscure, spreading at a broad angle (about 70°) from the midrib; sori crowded, greatly elongated, extending from midrib more than halfway to the margin; indusium narrow, elongated, extending the length of the sorus, pale green to yellow or whitish.

Asplenium sessilifolium Desv. Ges. Naturf. Freunde Berlin Mag. Neues. Entdeck. 5: 322. 1811. *A. sessilifolium* var. *guatemalense* Hieron. Bot. Jahrb. Syst. 34: 461. 1904 (type from Volcán de Agua, Sacatepéquez, *Lehmann 1480*). *A. guatemalense* Hieron. *loc. cit.*

In wet forests and wooded ravines and slopes, on the forest floor, or rarely on moss-covered boulders, 1,500-3,000 m.; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Santa Rosa; Sololá. Greater Antilles; Mexico; El Salvador; Nicaragua; Costa Rica; Colombia; Ecuador; Peru; Bolivia.

Plants terrestrial; rhizome erect to ascending, provided with linear or lanceolate, attenuate, castaneous scales, these clathrate, 3-5 mm. long; leaves pinnate, densely caespitose, 20-40 cm. long, 2.5-5 cm. broad; petiole wiry to stout, 3-12 cm. long, much shorter than the lamina, dull reddish or grayish brown, sparsely scaly (scales lanceolate at base, filiform above), abaxially terete, adaxially flattened or shallow-sulcate and sometimes marginate toward the lamina; lamina narrow-elliptic, glabrous, thin to firm-herbaceous, broadest near the middle, gradually reduced at both ends, the apex terminating in a pinnatifid, rarely proliferous apex; rachis glabrous or with a few scattered, filiform scales near the base, dull gray, or greenish or reddish brown, marginate or narrowly green-alate; pinnae 16-30 pairs, 1.5-3 cm. long, 0.6-1.2 mm. broad, sessile, crowded, horizontally spreading, obtuse, inequilateral at base, basiscopically cuneate to excavate, but acroscopically truncate and cut almost to the costa into a nearly free auricle (this often overlapping the rachis), the rest of the acroscopic margin singly or doubly, obtusely dentate, or with 1 or 2 shallow lobes adjacent to the auricle; veins simple to 1-forked (subflabellately branched in the auricle), commonly distinct, the tips scarcely enlarged, ending short of the pinna margin; sori medial to inframedial, linear, straight or slightly curved, 2.5-7 mm. long, 0.5-1 mm. broad; indusium delicate, linear, yellowish or hyaline, subentire.

Asplenium solmsii Bak. ex Hemsl. Biol. Centr. Amer. Bot. 3: 639. 1885.

On wooded slopes or in ravines, 1,200-1,500 m.; Quezaltenango; Sololá (type collection: cuesta de Atitlán, *Bernoulli & Cario 317*). Mexico (Chiapas).

Plants terrestrial; rhizome stout, erect, amply provided with linear, dark-brown, entire scales, these 0.1-0.5 mm. broad, obscurely clathrate, the cells crowded and elongated, with cell walls thick; leaves to 60 cm. long and 15 cm. broad, apparently nearly 3-pinnate (but not truly so, for the secondary segments are not completely free), caespitose; petiole stout, nearly equaling but commonly much shorter than the lamina, gray or gray-brown, terete abaxially, sulcate to trisulcate adaxially, sparsely scaly, the basal scales subclathrate as on the rhizome, those toward the lamina widely scattered, minute,

tortuous, and attenuate, mostly single-ribbed; lamina firm-herbaceous, ovate to oblong-lanceolate, tapering to a pinnatifid apex, slightly or not at all reduced at base, the tissue glabrous; rachis grayish brown, or yellowish distally, glabrous, or sparsely and minutely scaly as on the upper petiole, lacking proliferous buds; pinnae numerous, 5-8 cm. long, slightly ascending, approximate, subsessile or short-stalked, truncate or broadly cuneate and narrowly decurrent at base, attenuate at apex, cut nearly to the costa; secondary segments 12-20 pairs, decurrent and forming a broad wing along the costa, most of them again incised deeply into narrow, acute segments, each of these much longer than broad; veins simple, raised, and commonly distinct on both surfaces; sori 1 to each ultimate segment, elliptic, or at maturity nearly circular and extending beyond the acroscopic segment margin; indusium thin, pale yellow or whitish, linear, commonly 0.1-0.3 mm. broad (4-6 times longer than broad).

It may be that this is simply a more delicate form of *A. achilleifolium*. Besides the type, it is thus far known in Guatemala from one other collection (*Steyermark 33829*, Quezaltenango, January 1940). In addition, I have seen one collection from Chiapas (*Matuda 2637*). These specimens appear to differ from *A. achilleifolium* only in degree: smaller leaves, smaller and narrower indusia and rhizome scales, more deeply dissected pinnules, narrower ultimate segments. Further discussion may be found under *A. achilleifolium*.

Asplenium trichomanes-dentatum* L. Sp. Pl. 1080. 1753 (as *A. trichomanes dentatum*). *A. dentatum* L. Syst. Nat. ed. 10 (2): 1323. 1759. *nom. illeg.

In forests or thickets, on rocks or rocky walls, or ledges of cliffs, very rarely terrestrial, 100-500 m.; Izabal; Petén. Southern Florida; Yucatán; British Honduras; Honduras; West Indies; Colombia; Venezuela.

Plants epipetric, very rarely terrestrial; rhizome erect, provided with linear, clathrate, dark-brown to blackish scales, these 1-3 mm. long; leaves pinnate, fasciculate, dimorphous, the sterile ones shorter (3-9 cm. long), often spreading and forming a basal rosette, the fertile ones central, erect, 8-22 cm. long, 2-3 times longer than the sterile; petiole delicate, fleshy, flattened, sterile ones 0.5-2 cm. long, fertile ones 4-10 cm. long (often as long as the lamina), green to stramineous or brownish, nonalate, sometimes narrow-marginate, provided with a few, scattered scales and often some very minute, glandular trichomes; lamina linear or narrow-oblong, thin- to firm-herbaceous, essentially glabrous, but sometimes sparsely provided with scattered, very minute, glandular trichomes (especially on the margin), slightly reduced at base, terminating abruptly in a nonconform apical segment, not proliferous; rachis very sparsely provided with minute, glandular trichomes, greenish, narrow-alate (at least distally), flattened adaxially, but often appearing sulcate because of the perpendicular narrow wings; pinnae 6-10 pairs, rarely more than 12 mm. long and 8 mm. broad, at least the proximal ones short-stalked, spreading to slightly ascending, oblong to subtrapeziform, widely spaced (or those of sterile lamina crowded to imbricate), the apex obtuse to subacute, inequilateral at base, basiscopically cuneate or excavate, acroscopically truncate and often subauriculate, the margins crenate to serrate; veins simple to 1-forked, commonly distinct, the tips slightly enlarged, ending short of the margin; sori commonly 5-6 on a pinna, elliptic, 2-3 mm. long

and 1-1.5 mm. broad, often confluent at maturity and nearly covering the pinna surface; indusium delicate, yellowish, plane to revolute, subentire to slightly erose.

The nomenclature of this species has been confused since 1759, when Linnaeus, for reasons now unknown, changed the name of *A. trichomanes dentatum* (validly published in 1753) by eliminating the "*trichomanes*" and forming the binomial, *A. dentatum* L. One may theorize that Linnaeus sought to avoid confusion of epithets between this plant and *A. trichomanes* L. (a distinctive, black-petioled species), both of which were described on the same page in both publications. Up to the present time, authors have unanimously followed the latter course. Morton and Lellinger, in their treatment of the genus in Venezuela (Mem. New York Bot. Gard. 15: 241. 1966), noted that *A. trichomanes dentatum* could not be used, since the name had been "rejected universally as being confusing, not in binomial form, and probably due to an oversight on the part of Linnaeus." Only Proctor (Flora of the Lesser Antilles, Vol. 2, Pteridophyta: 314. 1977) has used the original name, hyphenated, and this, I believe, is the correct course of action. According to the rules of nomenclature, the name cannot be rejected as a trinomial, it is merely necessary to unite the specific epithets or join them with a hyphen (I.C.B.N. Art. 23, 1972). Neither can a name be rejected or modified merely because it is disagreeable or because another is preferable or better known (I.C.B.N. Art. 62, 1972).

***Asplenium tuerckheimii* Maxon, Contr. U.S. Natl. Herb. 13: 15. 1909.**

Not common, on slopes of wet, mixed forests, 300-1,400 m.; Alta Verapaz; Baja Verapaz (type from Panzál, *Tuerckheim II-1677*): Petén. Southern Mexico.

Plants evidently terrestrial; rhizome erect or ascending, sparsely provided at apex with minute, ovate, dark-brown scales, these 1-3 mm. long, often vaulted, clathrate, the cells small and mostly isodiametric; leaves pinnate, crowded or fasciculate, to 40 cm. long and 15 cm. broad; petiole stout, 1-2.5 mm. thick, 12-25 cm. long, sometimes longer than the lamina, dull gray or greenish to reddish brown, glabrous, subterete or flattened, shallow-sulcate adaxially, nonalate; lamina ovate or deltoid, firm-herbaceous, glabrous, scarcely or not reduced at base, terminating in a conform apical segment (or a subequal pair of segments), not proliferous; rachis glabrous, greenish or reddish gray, narrow-alate; pinnae 3-5 pairs, 5-9 cm. long, 1-1.8 cm. broad, at least the proximal ones stalked, widely spaced, ascending, lanceolate, acute or sometimes attenuate, narrowly cuneate at base, the margins broadly crenate-serrate; veins 1- or 2-forked, not very distinct, the tips slightly enlarged, ending short of the margin; sori mostly inframedial, linear or narrow-oblong, often slightly curved, 4-10 mm. long; indusium thin, narrow, yellowish brown.

This most closely resembles *A. falcinellum*. However the latter has

essentially entire pinnae, a nonalate rachis, filiform rhizome scales usually 4-5 mm. long, and sori which are mostly equidistant between costa and margin. *Asplenium tuerckheimii* has crenate-serrate pinnae, the rachis green-marginate or narrow-alate, shorter and broader rhizome scales (mostly 1 mm. long), and sori which are mostly nearer the costa than the margin.

***Asplenium williamsii* Stolze, Amer. Fern J. 68: 57. 1978.**

In wet forests, commonly on the forest floor, but rarely epiphytic, 1,250-2,300 m.; Alta Verapaz; Baja Verapaz; El Progreso (type from Montaña Canahui, 1,600-2,300 m., *Steyermark 43791*); El Quiché; San Marcos; Santa Rosa. Mexico (Chiapas).

Plants terrestrial, rarely epiphytic; rhizome stout, erect, amply provided with lanceolate or linear, lustrous, gray-brown, clathrate scales, these 4-6 mm. long, 0.5-0.8 mm. broad, mostly attenuate; leaves pinnate, subcaespitose, mature ones 15-45 cm. long, 4-6 cm. broad; petiole stout, 4-9 cm. long, much shorter than the lamina, dull gray or gray-brown, glabrous, abaxially terete, adaxially flattened and narrowly to broadly green-alate (especially toward the lamina), each of the wings 0.3-0.8 mm. broad; lamina linear to narrow-elliptic, glabrous, thin- to firm-membranaceous, slightly reduced at base, gradually reduced to a pinnatifid or serrate apex, not proliferous; rachis glabrous, dull gray or reddish brown, green-alate throughout; pinnae 14-20 (22) pairs, middle ones 2-3.5 cm. long, 0.8-1.5 cm. broad, sessile to short-stalked, spreading to slightly ascending, approximate to subdistant, oblong to lanceolate, obtuse to subacute, inequilateral at base, basiscopically cuneate or excavate, acroscopically truncate and often auriculate or subauriculate, the margins obtusely or subacutely serrate to biserrate; veins on acroscopic side commonly 1-forked, the basal one 2-forked, the distal ones and those of the basiscopical side simple, distinct adaxially, indistinct abaxially, the tips not or scarcely enlarged, ending well short of the margin; sori relatively long, often nearly reaching from midrib to margin (but tending to be more inframedial), linear, straight to slightly curved, 3-8 mm. long, 0.5-0.8 mm. broad, 1-2 proximal ones commonly double (diplazoid); indusium delicate, linear, pale yellowish to light brown, or hyaline, subentire.

This might be confused with *A. miradoreense*, but petioles of the latter are nonalate, or at least marginate or very inconspicuously alate just below the lamina, pinnae commonly number 20-35 pairs, and sori are relatively short and are nearly medial between costa and margin.

Asplenium williamsii may also be confused with *A. pteropus*, for both species have rather conspicuously alate petioles. However, the two may be rather easily distinguished by the characters used in the key.

DUBIOUS OR EXCLUDED SPECIES

***Asplenium blepharophorum* Bertoloni, Novi Comment. Acad. Sci. Inst. Bonon. 4: 403. 1840.** Type not seen: "Habitat in Vulcano d'acqua" (Volcán de Agua? on the border between Escuintla and Sacatepéquez),

collector and number not reported. Evidently known only from the description: "fronde bipinnata, foliolis pinnatifidis, laciniis obovatis, apice argute tridentatis, impari elongata, acuminata; paleis racheis ciliato-spinulosis." According to the description, this plant apparently belongs to the group of *A. solmsii-commutatatum-achilleifolium*, and, in the character of the "ciliate-spinulose" rachis scales, especially near *A. commutatatum*. Plants in this species complex are commonly found on slopes of volcanos in the chain of which Volcán de Agua is a part. Until the type is located, it would be fruitless to speculate further.

Asplenium cultrifolium L. Sp. Pl. 1081. 1753 (not Bory, 1803, Roxb. 1844, nor Griseb. 1864). Based on plate 59 of Plumier's "Traits des Fougères de l'Amerique," 1705. Various authors have referred to this species as being widely distributed in the neotropics, and a few specimens so identified have been found scattered in herbaria. Plumier's plate shows a rather large leaf from a creeping rhizome, with nonalate petiole and rachis, and the apical segment subconform (with two broadened basal lobes). The pinnae are broad, attenuate, with serrate margins, and four proximal ones have very strongly produced basal auricles on the acroscopic side. The sori are drawn with little concern for detail, for they can be construed as either single (asplenoid) or double (diplazoid). They are rather broad and straight and appear to lie along the central axis of a pinnate vein (which would be rather unique in an *Asplenium* of this type). Of all the Central American species, this plate most closely resembles *A. repandulum*. However, the pinnae of the latter are narrowly cuneate or excavate at base, basiscopically, whereas the Plumier illustration shows the basiscopic bases of all pinnae very broadly rounded. It is probably useless to further concern ourselves, for the truly diagnostic features of the original plant appear to have been carelessly illustrated, and Linnaeus's description offers no more conclusive evidence. Indeed, it may as readily be considered a species of *Diplazium*.

Asplenium erectum Bory ex Willd. in L. Sp. Pl., ed. 4, 5: 328. 1810. There is considerable speculation as to whether true *A. erectum* is to be found in the New World. Most American specimens under this name have been redetermined as *A. harpeodes*, but it remains for the monographer to determine the true classification of these taxa. Other Guatemalan species which form part of the complex are *A. miradorense*, *A. pteropus*, and *A. williamsii*. These, with a number of West Indian, South American, and Old World taxa, contribute to a confusing tangle of species and/or varieties, which can only be un-

raveled when the collections and types from around the world are all examined together.

Asplenium lunulatum Sw. J. Bot. (Schrader) 1800 (2): 52. 1801. Many neotropical collections are found in herbaria under this name. Guatemalan specimens so named are usually either *A. pteropus* or *A. harpeodes*, for true *A. lunulatum* is probably confined to South Africa. Even this is open to question, for as Hooker stated (Sp. Fil. 3: 128 [1860]), “. . . no authentic specimen nor any authentic intelligible description exists . . .” A fine discussion of the nomenclature was presented by Sledge in his treatment of the Ceylon species of *Asplenium* (Bull. Brit. Mus. [Nat. Hist.] Bot. 3: 248. 1965).

Asplenium obesum Bak. in Hook. & Bak. Syn. Fil. 209. 1867. Known only from the type (Volcán de Fuego, *Godman & Salvin* 119), this may be conspecific with *A. kellermanii*. I have not seen the type, but Baker described *A. obesum* as having a dark and lustrous petiole, a deltoid terminal “pinna,” and 4-6 broad, lateral ones, with texture coriaceous and venation flabellate. Of recognized species in Guatemala, this combination of features could only point to *A. kellermanii*, the type of which was collected in Sololá on Volcan Atitlan. This is only 35 km. from the type locality of *A. obesum* (Volcán de Fuego stands on the border between Escuintla and Chimaltenango). If the two are conspecific, the latter name, of course, has priority.

Asplenium otites Link, Hort. Reg. Bot. Berol. Descr. 2: 60. 1833. A number of Guatemalan collections reported under this name are merely small specimens of *A. pteropus*. *Asplenium otites* (perhaps = *A. pulchellum* Raddi) of southern Central America and South America is similar in leaf outline to these smaller plants, which have obtuse, subdimidiate pinnae. True *A. otites* has more strongly dimidiate pinnae, with veins mostly 1-forked on the dentate acroscopic side, and 1-3 unbranched veins on the subentire, basiscope side.

ATHYRIUM Roth

REFERENCES: F. K. Butters, The genus *Athyrium* and the North American ferns allied to *A. filix-femina*, *Rhodora* 19: 170-207. 1917. W. A. Sledge, The athyroid ferns of Ceylon, Bull. Brit. Mus. (Nat. Hist.) Bot. 2 (11): 275-323. 1962.

Plants terrestrial; rhizome stout and erect to slender and creeping, sparsely to amply scaly, the scales entire (in ours) to erose, light to dark brown, not or obscurely clathrate; leaves monomorphic (or occasionally subdimorphic due to the constriction of seg-

ments on fertile leaves), petiolate, of medium size (rarely to 1 m. long); petiole not articulate, glabrous, or somewhat scaly, especially at base, terete to somewhat flattened; lamina pinnate to 3-pinnate, essentially glabrous, but sometimes the axes bearing scattered septate trichomes or filamentous scales, texture thin-membranaceous to sub-chartaceous, lanceolate to ovate, commonly tapering to a pinnatifid apex, lacking proliferous buds; pinnae several to many, alternate (but in a few species some of them subopposite), sessile to stalked, equilateral to inequilateral at base; venation free, anadromous, the veins simple or branched, terminating near or somewhat short of the margin; sori linear to elliptic, borne along the vein, many straight (asplenoid) but many also (at least in ours) distally hooking across the vein and partially doubling back on the other side, or in some species (outside our area) reniform; indusia commonly present, membranaceous, light brown to scarious, of the shape of the sorus, attached along the vein, margins entire to erose or fimbriate, often glandular; paraphyses lacking; sporangium slender-stalked, composed of 2-3 rows of cells (at least distally), commonly glabrous; spores monolete, ellipsoid to reniform, with or without perine.

Athyrium is a nearly cosmopolitan genus of 150-200 species, chiefly found in temperate regions. These terrestrial ferns are typically of medium size, with thin leaves and fragile petioles. The relationship of this genus to others is still the subject of controversy, as is the circumscription of many of its species. Some workers have tended to combine at least *Athyrium* and *Diplazium*, and indeed the morphological differences between many of their species are not sharp. However (although cytological studies are far from complete) all three genera seem to differ in their chromosome base numbers: that of *Asplenium* typically 36, of *Athyrium* 40, of *Diplazium* 41. In Guatemala, the soral characters of both species of *Athyrium* are sufficiently distinct so that there is no great problem separating them from our species of *Diplazium*.

For further discussion of these closely related genera, see treatment of *Asplenium*.

- a. Pinnae 6-10 free pairs; lamina thin-membranaceous, pinnate-pinnatisect; rhizome slender, long-creeping, with scales mostly 2-3 mm. long and 0.2-0.4 mm. broad.

A. skinneri.

- a. Pinnae numerous; lamina firm-herbaceous to chartaceous, 2-pinnate to 2-pinnate-pinnatisect; rhizome stout, short-creeping to somewhat ascending, with scales mostly 4-7 mm. long and 0.8-2 mm. broad. *A. dombei*.

Athyrium dombei Desv. Prodr. (Mém. Soc. Linn. Paris VI): 266. 1827. *Asplenium dombeyi* (Desv.) Mett. Ann. Sci. Nat. Bot. V: 2: 238. 1864. *Athyrium filix-femina* (L.) Roth var. *dombeyi* Hieron. Bot. Jahrb. Syst. 34: 456. 1904.

In forests, thickets, and wooded ravines, 1,300-3,000 m.; Alta Verapaz; Huehuetenango; El Quiché; San Marcos; Totonicapán. Southern Mexico; British Honduras; Costa Rica; Colombia; Venezuela; Peru; Bolivia; Argentina.

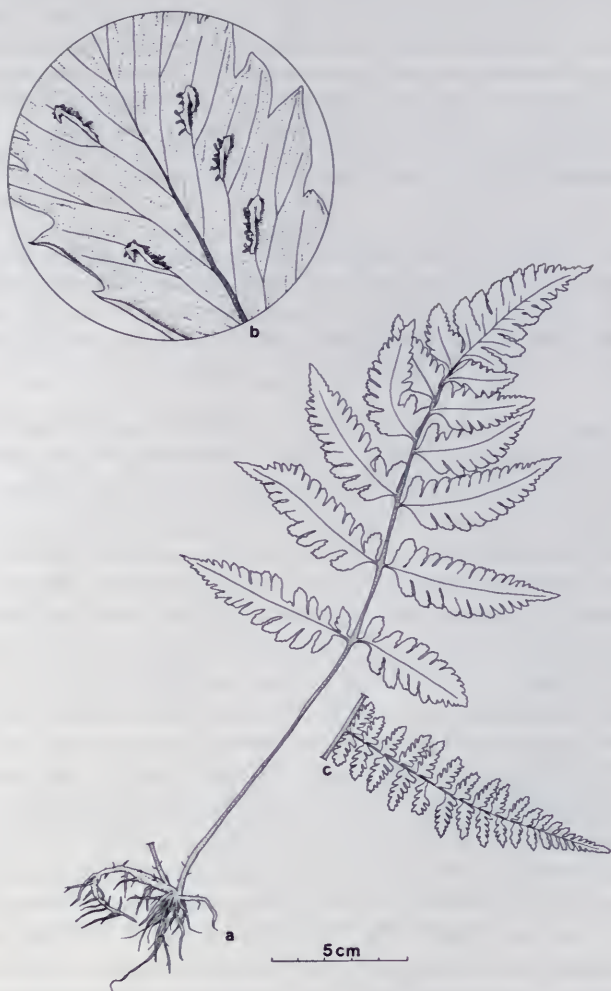


FIG. 12. *Athyrium*. a-b, *A. skinneri*: a, habit, $\times \frac{1}{2}$; b, portion of pinnule with sori, $\times 7$; c, *A. dombei*, pinna, $\times \frac{1}{2}$.

Plants terrestrial; rhizome stout, short-creeping to somewhat ascending, sparsely to abundantly provided with light- to dark-brown, lanceolate to ovate scales, these 4-7 mm. long, 0.8-2 mm. broad; leaves 45-100 cm. long, 7-30 cm. broad, 2-pinnate to nearly 3-pinnate, densely crowded to subfasciculate; petiole slender to stout, 12-50 cm. long, $\frac{1}{2}$ the length of, to nearly equaling, the lamina, drying stramineous to light brown (or darker at base), subterete to angular, usually flattened when dried, sparsely scaly, or often amply so at base, the scales light to dark brown, lanceolate, 5-10 mm. long, 1-2 mm. broad; lamina firm-herbaceous to chartaceous, lanceolate to broadly ovate, tapering to a pinnatifid apex, scarcely to somewhat reduced at base, glabrous, or the axes sparsely provided with filamentous scales abaxially; pinnae numerous, sessile to short-stalked, alternate, crowded to subdistant, lanceolate, acute to attenuate at apex, mostly truncate at base, pinnate to nearly 2-pinnate, larger ones 5-20 cm. long, 1.5-6 cm. broad; pinnules 12-22 pairs, elliptic- to deltoid-lanceolate, subentire or serrate to very deeply pinnatisect; veins free, distinct to obscure, several-forked to pinnately arranged in the ultimate segments, terminating at or near the margin; sori 4-10 (-12) pairs to a pinnule, often confluent at maturity, about $\frac{1}{2}$ of them asplenioid and $\frac{1}{2}$ athyroid, mature ones 0.8-1.5 mm. long; indusium usually thin, yellowish to brown, or often scarious, the margin erose to ciliate, the cilia frequently glandular and commonly deciduous at maturity.

Taxonomy of the *A. filix-femina* (L.) Roth complex has long been, and remains, annoyingly perplexing. There have been several fine studies (e.g., Butters, 1917) attempting to treat the various species, varieties, and forms in a rather limited, regional perspective, as well as countless publications manipulating the ranks of taxa within the complex. Unfortunately none of these has been very effective, for the "Lady Fern" is a plant with such a highly variable morphology and such a wide pattern of distribution around the earth that only a comprehensive study of worldwide collections will suffice to unravel the taxonomic problems (quite comparable to those which once plagued *Pteridium aquilinum*). Depending on the author, the "Lady Fern" may be treated as one to a dozen different species, and as scores of infraspecific taxa. In the Old World the tendency has been to accept the number of variants as varieties and forms of *A. filix-femina*, and in the New World the trend has been toward recognizing them as different species, all in turn with their own varieties and forms. In U.S. herbaria one will commonly find collections of neotropical "Lady Ferns" under such names as *A. asplenioides* (Michx.) Eaton, *A. bourgaei* Fourn., *A. dombei* Desv., *A. martensii* (Kze.) Moore, and *A. michauxii* (Spreng.) Fée.

Characters traditionally used to separate taxa within the complex are: degree of dissection of lamina; point at which lamina is widest; relative length of petiole; relative size and color of petiole or rhizome scales; relative length of basal pinnae; proportion of asplenioid *vs.* athyroid sori; character of cilia and glands on indusium margin. Unfor-

tunately for the taxonomist, the only thing consistent about these features is their inconsistency, so one is led to infer that any separation of taxa would be best set at the infraspecific level. For purposes of this Flora I choose to recognize the "Lady Ferns" of Guatemala as *A. dombei*. My personal feeling is that this might better be considered a variety of *A. filix-femina* (indeed, some of the specimens examined are very difficult to distinguish from var. *asplenioides* [Michx.] Farwell). However, *A. dombei* seems to be the name most often used by current authors, and until a complete revision of the complex is attempted, this one is as good as any.

Athyrium skinneri (Bak.) Diels in Engl. & Prantl, Nat. Pflanzenfam. 1 (4): 244. 1899 (type from Guatemala, location undescribed, *Skinner s.n.*). *A. skinneri* Moore, Index Fil. 187. 1860. *nom. nud.* *Asplenium skinneri* Bak. in Hook. & Bak. Syn. Fil. 226. 1867.

Rare, in wet forests or wooded ravines, 900-1,200 m.; Santa Rosa. Mexico; El Salvador; Nicaragua; Costa Rica.

Plants terrestrial; rhizome slender, long-creeping, sparsely provided with orange to light-brown, lanceolate or linear-lanceolate scales, these 2-3 mm. long and 0.2-0.4 mm. broad; leaves 30-50 cm. long, 12-22 cm. broad, pinnate-pinnatisect (in ours) to (very rarely) 2-pinnate-pinnatifid, crowded to subdistant on the rhizome; petiole weak and succulent, often swollen at base, 12-24 cm. long, shorter than the lamina, green, drying yellow or light brown, subterete to angular, usually flattened when dried, sparsely scaly, the scales as on the rhizome, but somewhat longer; lamina thin-membranaceous, ovate to deltoid-ovate, tapering to a pinnatifid apex, slightly or not reduced at base, essentially glabrous, but rarely some scattered hairlike scales on the axes abaxially; rachis drying yellow or yellow-brown, glabrous or with scattered, minute, septate trichomes, flattened when dried; pinnae 6-10 free pairs, 6-10 cm. long, 2-3 cm. broad, often subopposite (especially the proximal ones), crowded to subdistant, short-stalked, narrowly to broadly lanceolate, acute to attenuate at apex, truncate (acroscopically) to broadly cuneate at base, incised deeply to the broad costal wing (or sometimes at base cut quite to the costa); secondary segments 12-16 pairs, serrate, or larger ones incised; veins free, distinct, pinnately arranged in the segments, the branches simple or 1- to 2-forked, the tips ending just short of the margin; sori commonly 4-6 to each segment, most of them asplenioid, but many athyroid, borne midway between midrib and margin, mature ones 0.5-1.5 mm. long; indusium thin, the margin erose to ciliate.

This is a rather rare fern, not well represented in herbaria. Most specimens I have examined are remarkably constant in their morphological characters, especially in shape, size, and dissection of pinnae. However, I have seen three collections which may well represent a distinct variety of the species (*Mexia 533*, Nayarit, Mexico: *Standley 79830*, Chimaltenango; *Williams & Molina 16731*, El Salvador). These are typical of *A. skinneri* in every way, but the leaves are much longer and broader, and the pinnae are fully pinnate-pinnatifid. Only the

Mexia specimen bears a small portion of the rhizome (slender and long-creeping), and I hesitate to describe a new variety based on such scanty material.

BLECHNUM Linnaeus

REFERENCES: Jean Broadhurst, The genus *Struthiopteris* and its representatives in North America, Bull. Torrey Bot. Club 39: 257-278; 357-385. 1912. M. T. Murillo, *Blechnum* subgenero *Blechnum* en sur America, Nova Hedwigia XVI: 329-366, and t. 110-147. 1968.

Plants commonly terrestrial, but some species scandent high up on the trunks of trees; rhizome scaly, commonly ascending to erect, sometimes wide-creeping and scandent, occasionally very stout and epigeous, rarely subarborescent; leaves dimorphous or monomorphous, medium-sized to quite large, the axes often scaly; petiole not articulate, sparsely scaly, terete or flattened abaxially and sulcate adaxially; lamina commonly pinnate or pinnatifid, rarely simple or 2-pinnate, fertile ones greatly contracted or similar to the sterile; pinnae continuous with, rarely articulate to, the rachis, fertile ones having the same shape as the sterile, or greatly constricted, the margins entire to serrate; veins of sterile segments free (at least in ours), simple to usually 1-forked, in fertile segments connected by a vascular commissure which runs parallel to the costa and to which is attached the sorus; sori linear, commonly uninterrupted, parallel, one on each side of, and near or against, the costa; indusium persistent, linear, opening toward the costa, on segments of greatly constricted lamina appearing marginal; sporangia long-stalked, copious, often forming an uninterrupted mass between costa and point of attachment of the indusium; spores monolete, bilateral, with perine.

Sporadically, for nearly two centuries, the genus has been split by various authors into a dozen or more genera, and then as frequently reunited under *Blechnum*. The most familiar of these are *Struthiopteris* Weiss and *Lomaria* Willd., under which have been placed the species with strongly dimorphous leaves. I prefer to follow the treatment of Copeland (Gen. Fil., 1947) because within the genus *Blechnum*, *sens. lat.* ". . . the contraction of the fertile pinnae ranges from incipient and inconstant to apparently complete absence of sterile surface" Copeland maintained the neotropical *B. volubile* Kaulf. in the monotypic genus *Salpichlaena*. This species does not occur in Guatemala.

Blechnum is a pantropical genus, with strong representation in both hemispheres, and a few of its species even occur in temperate zones. In the aggregate sense, *Blechnum* contains nearly 200 species, many of them nebulously circumscribed. A good revision, on a worldwide basis, is urgently needed, after which I suspect the total number of species could be reduced by 10-20 percent.

- a. Leaves monomorphous or essentially so, the segments of fertile laminae not or only slightly more constricted than those of the sterile.

- b. Pinnae articulate at the rachis; rhizomes long-creeping. *B. serrulatum*.
- b. Pinnae not articulate; rhizomes erect to ascending.
 - c. Lamina gradually and conspicuously tapering to base; proximal pinnae (several to many pairs) greatly shortened, the lowermost 1-3 pairs often reduced to mere auricles.
 - d. Leaves over 50 cm. long and 20 cm. broad; pinnae mostly ascending, larger middle ones 8-22 cm. long and 1-2.2 cm. broad, with margins commonly undulate. *B. brasiliense*.
 - d. Leaves 8-46 (60) cm. long, 1.6-8 cm. broad; pinnae spreading, larger middle ones 1-4 cm. long and 0.2-0.8 cm. broad, with margins plane. *B. polypodioides*.
 - c. Lamina not or scarcely reduced at base; proximal pinnae (1-3 pairs) only slightly shortened, or rarely the basal pair half as long as the longest central ones.
 - e. Pinnae 1-8 (10) pairs; lamina terminating abruptly in a subconform apical segment, this longer than the longest pinnae and commonly as long or longer than the rest of the lamina. *B. fraxineum*.
 - e. Pinnae 12-26 pairs; lamina gradually tapering to a pinnatifid or subcaudate apex.
 - f. Rachis glabrous on both sides; alt. 50-1,000 (1,300) m. *B. occidentale* var. *occidentale*.
 - f. Rachis sparsely to densely glandular-pubescent abaxially; alt. 1,200-2,700 m. *B. occidentale* var. *pubirhachis*.
- a. Leaves dimorphous, the segments of fertile laminae greatly constricted.
 - g. Sterile lamina fully pinnate, most pinnae stalked, not adnate; rachis and costae sparsely to abundantly scaly; pinna margins entire to serrate.
 - h. Pinna margin sharply and conspicuously serrate throughout; costa amply to abundantly scaly. *B. falciforme*.
 - h. Pinna margin entire (but serrulate near apex); costa commonly sparse-fibrillose or scaly (the scales sometimes early deciduous).
 - i. Pinnae commonly cordate or subcordate at base. *B. costaricense*.
 - i. Pinnae commonly tapered to broadly rounded at base. *B. schiedeanum*.
 - g. Sterile lamina pinnatisect, or if pinnate, the pinnae sessile, adnate, never stalked; rachis and costae essentially lacking scales; pinna (segment) margins entire.
 - j. Rhizome scales linear, rigid, often bicolorous (at least the older ones with a dark, narrow, median stripe), margins sparsely to copiously setose or setulose; plants scandent on tree trunks, the rhizome greatly elongated.
 - k. Sterile lamina (14-) 18-32 cm. broad, scarcely or not reduced at base; larger fertile pinnae 8-18 cm. long, 1.5-4 mm. broad; rhizome scales sparsely and minutely setulose. *B. ensiforme*.
 - k. Sterile lamina 4-8 (-12) cm. broad, tapering strongly and gradually to base; larger fertile pinnae 3-6 cm. long, 0.5-1.8 mm. broad; rhizome scales copiously and conspicuously setose. *B. fragile*.
 - j. Rhizome scales lanceolate to ovate, often flaccid, concolorous, margins subentire; plants terrestrial, the rhizome erect to ascending, or short-creeping and stoloniferous.
 - l. Sterile lamina slightly or not at all reduced at base, or abruptly reduced to 1-3 pairs of lobes or auricles; sterile leaves (10) 12-30 cm. broad, their petioles (8) 12-40 cm. long and provided with scattered, scalelike or scarlike vestigial pinnae; fertile leaves 11-20 cm. broad. *B. divergens*.
 - l. Sterile lamina tapering strongly and gradually to base, the proximal 4-12 pairs

of segments greatly reduced; sterile leaves 1.5-8 (9) cm. broad, their petioles 0.5-10 cm. long, lacking scalelike or scarlike vestigial pinnae (not to be confused with the basal, auriculiform segments); fertile leaves 1.2-7 cm. broad.

- m. Rhizomes ascending to erect, commonly becoming an epigeus caudex to 40 cm. long and 1.5 cm. thick, lacking stolons; sterile leaves 20-45 cm. long; fertile leaves 3.5-7 cm. broad, with petiole 10-22 cm. long. *B. lehmannii*.
- m. Rhizome short-creeping to ascending, stoloniferous; sterile leaves 6-18 (20) cm. long; fertile leaves 1.2-2.2 cm. broad, with petiole 2.2-6 cm. long. ...

B. stoloniferum.

Blechnum brasiliense Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 330. 1811. *B. corcovadense* Raddi, Opusc. Sci. 3: 294. 1819.

Apparently known in Central America only from a single Guatemalan collection: swampy thickets, Montaña Castilla, 3 mi. southeast of Quezaltepeque, alt. 1,200-1,500 m., Depto. Chiquimula (*Steyermark 31347*, 1939). Colombia; Brazil; Peru; Bolivia; Argentina; Paraguay; Uruguay.

Plants terrestrial; rhizome stout, erect, densely scaly, the scales linear to lanceolate, light to dark brown or blackish; leaves rigid, erect, monomorphic, 50-120 cm. long, 20-40 cm. broad, short-petiolate; petiole 2-12 cm. long, subterete abaxially, sulcate adaxially, light to dark brown, or blackish at base, densely provided at base with linear or linear-lanceolate scales, these orange to brown or lustrous black, commonly tortuous, with filiform tips; lamina pinnate or very deeply pinnatisect, chartaceous to subcoriaceous, glabrous, narrow-elliptic, broadest at or near the middle, tapering gradually to a pinnatifid apex, reduced gradually and conspicuously at base; rachis stramineous to light brown, essentially glabrous, prominulous and terete or subquadrangular abaxially, sulcate adaxially; pinnae (or segments) numerous, most of them ascending, elongate-deltoid, acute at apex, adnate to the rachis at base, the margins commonly undulate and strongly serrate or serrulate (the teeth often subcartilaginous and spinulose), proximally becoming gradually and conspicuously shorter and more obtuse, with the lowermost 1-3 pairs often reduced to mere auricles, the larger, middle ones 8-22 cm. long and 1-2.2 cm. broad; veins distinct, commonly 1-forked near the costa, the tips not or scarcely enlarged, terminating at the margin; sori not usually borne on the strongly reduced, proximal pinnae; indusium subentire, firm, sometimes undulate, but rarely splitting at maturity, attached 0.2-0.6 mm. from the costa.

The species is aptly named, as it is far more abundant in Brazil than anywhere else. It is found as far north as Colombia but heretofore has not been found in the West Indies, or in Central America except for the one Steyermark specimen collected in Chiquimula in 1939. This is curious, in that the plants are large and conspicuous and not likely to be overlooked even by general collectors. It should not be confused with any other Guatemalan species.

Blechnum costaricense (Christ) C. Chr. Index Fil. 152. 1905. *Lomaria costaricensis* Christ, Bull. Herb. Boissier II. 4: 1092. 1904.

Struthiopteris costaricensis (Christ) Broadh. Bull. Torrey Bot. Club 39: 363. 1912.

In wet forests and shaded ravines, sometimes growing on fallen tree trunks, 1,300-2,200 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; El Progreso; El Quiché; San Marcos. Southern Mexico to Panama.

Plants terrestrial; rhizome relatively small, erect, this and the petiole base amply provided with lanceolate, attenuate, flaccid scales, these light brown or tawny, to 2 cm. long and 0.4 cm. broad; leaves erect, fully pinnate, to 1.3 m. long and 0.3 m. broad, dimorphous, long-petiolate; petiole to 70 cm. long, stramineous to light brown, rarely dark brown at base, the scales above the base sparse and often fugacious, these linear or linear-lanceolate, to 2 cm. long, flaccid, dirty-white to light brown and commonly intermixed with minute orange scurf; lamina lanceolate or elliptic-lanceolate, coriaceous or subcoriaceous, not or scarcely reduced at base, gradually reduced at apex and terminating in a free, conform apical segment; rachis stramineous to light brown, abaxially with a conspicuous, fusiform, castaneous aerophore at the base of each pinna, sparsely to amply scurfy and scaly. Sterile pinnae 12-20 pairs, 12-22 cm. long, 1.7-2.5 cm. broad, linear-lanceolate, falcate to nearly straight, acuminate at apex, most (or at least the proximal ones) short-stalked, cordate to subcordate at base, the margins strongly revolute, entire, but serrate at apex, glabrous, or the veins sometimes with a few scattered, minute scales abaxially; costae abaxially stramineous, strongly prominulous, naked to sparsely scaly or fibrillose, adaxially glabrous or essentially so, sulcate, or at least appearing so because of the parallel, raised, often cartilaginous ridges flanking it on either side; veins simple or 1-forked, terminating at pinna margin, abaxially distinct, somewhat prominulous, adaxially indistinct, the tips not or slightly enlarged and discolored. Fertile pinnae short-stalked, larger ones 12-22 cm. long, 0.2-0.4 cm. broad, the base truncate or cordate; costa glabrous, or sparsely scaly abaxially; indusium light or dark brown, strongly erose, and often deeply lacerated.

It is with great reluctance that I maintain this and *B. schiedeana* as distinct species. The only character separating the two is that of shape of pinna base, and this is not always an obvious distinction. Thus it would be more appropriate to recognize them as varieties. However, these comprise only part of a large and confusing complex that exists in the neotropics (and perhaps in the paleotropics as well). Some of the better-known South American names are *B. cordatum* (Desv.) Hieron., *B. ornifolium* (Presl) Ettingsh., and *B. raddianum* Rosenst. I have not seen the types of all species involved and am not qualified to make such a taxonomic decision at this time, but future monographic study will certainly show that all the above taxa should be lumped together under *B. cordatum* (some perhaps as forms or varieties).

Blechnum divergens (Kunze) Mett. Ann. Sci. Nat. Bot. V. 2: 255. 1864. *Lomaria divergens* Kunze, Linnaea 9: 57. 1834. *L. exaltata* Fée Mém. Fam. Foug. 11: 10, t. 3. 1866. *Struthiopteris exaltata* (Fée) Broadh. Bull. Torrey Bot. Club 39: 264. 1912.

In wet forests, on the forest floor, often at bases of trees; 1,600-2,400

m.; Baja Verapaz; San Marcos. West Indies; southern Mexico; Honduras; Nicaragua; El Salvador; Costa Rica; Panama; Colombia to Peru.

Plants terrestrial; rhizome ascending to erect, commonly becoming an epigeous caudex, to 30 cm. long and 2 cm. thick, sparsely to amply scaly, the scales 5-12 mm. long, light brown, concolorous, flaccid, lanceolate to ovate, the margins subentire; leaves subfasciculate at rhizome apex, petiolate, dimorphous. Sterile leaves deeply pinnatisect, 40-90 cm. long, (10-) 12-30 cm. broad; petiole (8) 12-40 cm. long, stout, castaneous to atropurpureous (very rarely yellowish brown), subterete, flattened, or angular, glabrous or sparsely scaly, provided with scattered vestigial, scalelike pinnae usually somewhat distant from the base of the lamina; lamina essentially glabrous, broadly lanceolate, ovate, or deltoid-ovate, tapering gradually to a subconform apical segment, scarcely or not at all reduced at base (although sometimes with 1-3 pairs of greatly reduced, auriculiform pinnae descending from lamina base); texture chartaceous to coriaceous; rachis yellowish brown to castaneous, terete and slightly to strongly prominulous abaxially, sulcate adaxially; segments 12-22 pairs, elongate-triangular to broadly ensiform, subfalcate, narrowly acute, larger ones 3.5-7 times as long as broad, joined at or near the rachis by an acute to broadly rounded sinus, the proximal 1-2 pairs slightly or not at all reduced, but sometimes several greatly reduced, auriculiform lobes extending from the basal segments down along the petiole and gradually merging into the scalelike, vestigial pinnae, margins entire, plane to revolute; veins indistinct or obscure, simple or (more commonly) 1-forked at or near the base, terminating short of the margin, their tips strongly and abruptly dilated and discolored. Fertile leaves pinnate, (40) 70-100 cm. long, 11-20 cm. broad; petiole (18) 32-50 cm. long, castaneous to atropurpureous, commonly provided for most of its length with vestigial, scalelike pinnae; lamina broad-lanceolate to deltoid-ovate, rather abruptly terminating in a caudate apical segment, scarcely reduced at base, rachis yellowish brown to castaneous; pinnae glabrous, linear, greatly constricted, larger ones 8-12 cm. long, 0.25-0.4 cm. broad, sessile, adnate to rather strongly decurrent; indusium narrow, commonly erose.

This is closely related to *B. lehmannii*, and young plants of each species are easily confused. Further comparisons are made under the discussion of the latter.

Blechnum ensiforme (Liebm.) C. Chr. Index Fil. 153. 1905. *Lomaria ensiformis* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 234 (seors. 82). 1849. *Struthiopteris ensiformis* (Liebm.) Maxon, Contr. U.S. Natl. Herb. 13: 17. 1909.

In wet forests and wooded ravines, scandent on tree trunks and stumps, 1,000-2,300 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Quezaltenango; San Marcos. Southern Mexico; Honduras to Panama; Colombia; Ecuador; possibly Peru and Bolivia.

Plants scandent; rhizome stout, cordlike, greatly elongated, amply to densely scaly, the scales 0.5-1 cm. long, rather rigid, linear-lanceolate, commonly attenuate, with margins sparsely and minutely setulose (the setae often deciduous), deep amber to dark brown, often (especially on older scales) bicolorous, with a narrow, blackish median stripe; leaves approximate to widely spaced, petiolate, dimorphous. Sterile leaves deeply pinnatisect, or fully pinnate in the proximal half, commonly 50-100 cm. long, (14-) 18-32 cm. broad; petiole 10-28 cm. long, much shorter than the lamina, stout,

yellowish brown and sulcate adaxially, reddish brown to atropurpureous and terete abaxially, essentially glabrous, commonly provided with a few, scattered, vestigial pinnae near base of lamina; lamina glabrous, chartaceous to subcoriaceous, lanceolate- to deltoid-ovate, tapering gradually to a subentire apical segment, scarcely or not reduced at base; rachis glabrous, adaxially sulcate and stramineous to yellowish or grayish brown, abaxially terete and yellowish brown to (proximally) reddish brown to atropurpureous; pinnae (or segments) numerous, ensiform, straight or subfalcate, long-acuminate, margins entire, plane or slightly revolute, distal ones dilated at base and joined to adjacent ones by a narrow to broad sinus, proximal ones commonly free, subdistant, sessile, dilated to slightly contracted at base, the basal 1-3 pairs slightly or not at all reduced; veins distinct to indistinct abaxially, indistinct to obscure adaxially, simple, or 1-forked at base, terminating near the margin, their tips somewhat enlarged. Fertile leaves pinnate, 50-90 cm. long, 15-30 cm. broad; petiole 12-28 cm. long, stramineous to reddish brown, often with a few, vestigial, scarlike pinnae near base of lamina; lamina ovate or deltoid-ovate, gradually tapering to a caudate apical segment, reduced abruptly at base; rachis stramineous to light brown, glabrous, or sparsely and minutely scaly; pinnae glabrous, linear, greatly constricted, larger ones 8-18 cm. long, 0.15-0.4 cm. broad, sessile, adnate, slightly dilated or contracted at base; indusium very narrow, subentire.

This is closely related to *B. fragile*, from which it is distinguished primarily by size and shape of leaf. However, more than a few specimens have been observed in Guatemala and Honduras which are intermediate in the width and taper of their laminae. Other than the characters used in the key, the two may often be separated also by degree of dissection of the sterile lamina. In *B. fragile* the leaf is deeply pinnatisect, and a few free pinnae (if any) are present only at the very base of the lamina. In *B. ensiforme*, leaves (especially larger ones) are often fully pinnate in the proximal third, with many lower pinnae 2-3 cm. apart.

Blechnum falciforme (Liebm.) C. Chr. Index Fil. 154. 1905. *Lomaria falciformis* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 234 (seors. 82). 1849. *Struthiopteris falciformis* (Liebm.) Broadh. Bull. Torrey Bot. Club 39: 365. 1912.

In wet forests, thickets, and shaded ravines, often on steep to vertical banks, 2,000-3,200 m.; Chimaltenango; Chiquimula; Huehuetenango; Jalapa; Quezaltenango; El Quiché, San Marcos. Mexico; Honduras; El Salvador; Costa Rica; Panama; Colombia; Ecuador.

Plants terrestrial; rhizome stout, erect, densely scaly, the scales lanceolate to ovate, flaccid, orange to dark brown, to 1.5 cm. long and 0.5 cm. broad; leaves erect, fully pinnate, to 2.2 m. long, dimorphous, long-petiolate; petiole to 50 cm. long, stramineous to reddish brown, or atropurpureous at base, sparsely to densely scaly, the scales often deciduous above the base, dirty-yellow to castaneous, to 3 cm. long, filiform to ovate, flaccid, with attenuate tips, and commonly intermixed with minute orange scurf; lamina lanceolate or elliptic-lanceolate, 50 cm. broad, chartaceous to subcoriaceous, not or scarcely reduced at base, gradually reduced at apex and terminating in a free, conform,

apical segment; rachis stramineous to yellow-brown, abaxially with a conspicuous, fusiform, castaneous aerophore at base of each pinna, sparsely to amply scurfy and scaly, the scales often deciduous, much like those of the petiole, but smaller. Sterile pinnae numerous, spreading or ascending, linear to lanceolate, falcate to nearly straight, acuminate at apex, most of them short-stalked (1-4 mm.) and broadly rounded to subcordate at base, the margins plane, or sometimes revolute, sharply and conspicuously serrate, the serrations to nearly 1 mm. long, sharp, cartilaginous, strongly curved toward pinna apex (or even incurved), the surface and veins abaxially often scurfy and minutely scaly; costae abaxially stramineous, prominulous, amply to densely orange-scaly, adaxially glabrous or nearly so, sulcate, or at least appearing so because of the parallel, raised, often cartilaginous ridges flanking it on either side; veins simple or 1-forked, terminating at the pinna margin, abaxially distinct, somewhat prominulous and with orange, filamentous scales sparse or lacking, adaxially indistinct, the tips commonly enlarged and discolored. Fertile pinnae subsessile to short-stalked (1-5 mm.), larger ones 10-22 mm. long, 3-6 mm. broad, the base broadly rounded to cordate; costa on abaxial side amply provided with orange to light-brown, ovate scales; indusium castaneous, strongly erose, and often deeply lacerated.

Blechnum fragile (Liebm.) Morton & Lell. Amer. Fern J. 57: 68. 1967. *Osmunda polypodioides* Sw. Nov. Gen. Sp. Pl. Prodr. 127. 1788. *B. onocleoides* Sw. J. Bot. (Schrader) 1800 (2): 75. 1801. *nom. illeg.* *Onoclea polypodioides* (Sw.) Sw. Fl. Ind. Occ. 3: 1585. 1806 (not L. 1771). *Lomaria polypodioides* (Sw.) Desv. Mem. Soc. Linn. Paris 6: 288. 1827 (not Gaud. 1825). *L. onocleoides* Spreng. in L. Syst. Veg. ed. 4 (4): 62. 1827. *Spicanta onocleoides* (Spreng.) Presl, Epim. Bot. 114. 1849. *Lomaria fragilis* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 232 (*seors.* 80). 1849. *B. polypodioides* (Sw.) Kuhn, Fil. Afric. 92. 1868 (not Raddi, 1819). *Struthiopteris polypodioides* (Sw.) Trev. Atti Ist. Veneto III. 14: 571. 1869. (The nomenclature of this plant was long confused with that of *B. polypodioides* Raddi. Morton and Lellinger [1967] have fully clarified the matter.)

In wet forests and shaded ravines, scandent on tree trunks, 1,300-2,800 m.; Alta Verapaz; Baja Verapaz; Quezaltenango; El Quiché; San Marcos. Southern Mexico; Honduras; Nicaragua; Costa Rica; Panama; West Indies.

Plants scandent; rhizome rather stout, greatly elongated, densely scaly, the scales 0.5-1.5 cm. long, rather rigid, linear to linear-lanceolate, attenuate, with margins copiously and conspicuously setose, amber to dark brown, often (especially on older scales) bicolorous, with a narrow, blackish median stripe; leaves approximate to subdistant, petiolate, dimorphous. Sterile leaves deeply pinnatisect (juvenile ones sometimes subentire to lobed), 25-65 cm. long, 4-8 (-12) cm. broad; petiole 6-12 cm. long, much shorter than the lamina, wiry to stout, yellowish or reddish brown and sulcate adaxially, reddish brown to atropurpureous and terete abaxially, essentially glabrous, commonly provided with a few, scattered, vestigial pinnae near base of lamina; lamina glabrous, linear to lanceolate, tapering strongly but gradually at both ends, terminating in a subentire apical segment, texture firm-herbaceous to chartaceous or (rarely) subcoriaceous; rachis

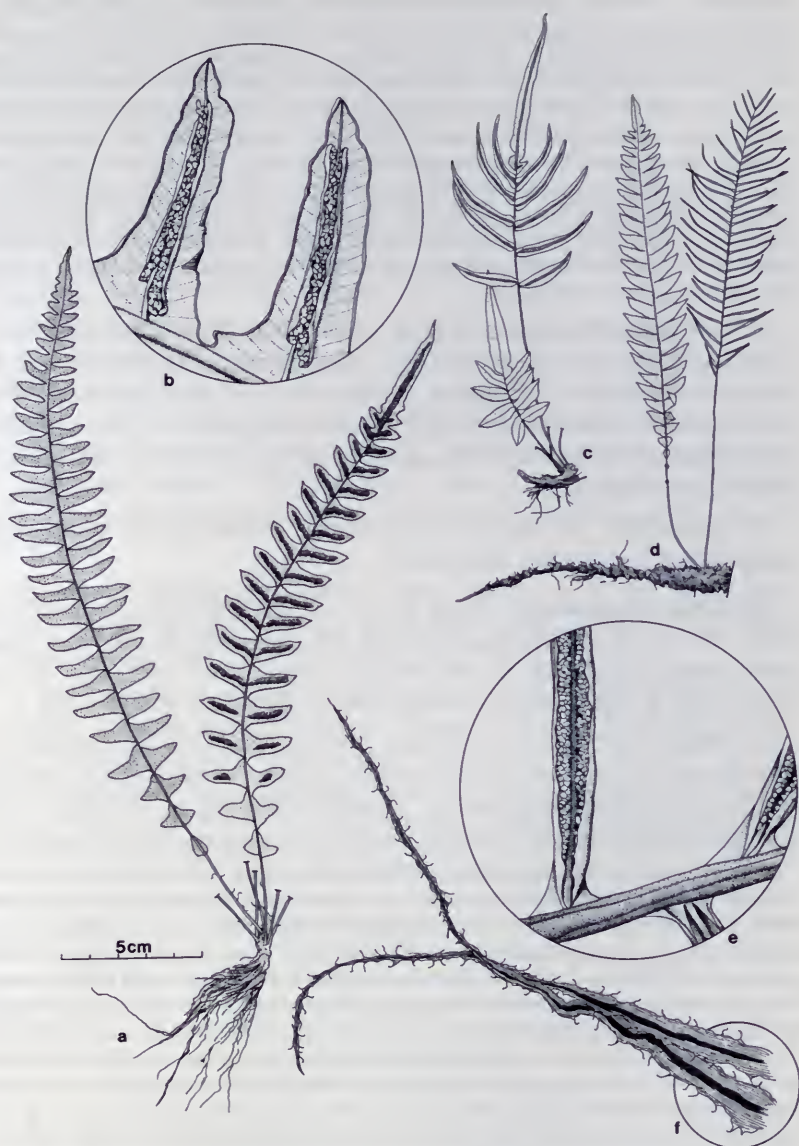


FIG. 13. *Blechnum*. a-b, *B. polypodioides*: a, habit, $\times \frac{1}{2}$; b, rachis and pinnae, $\times 3\frac{1}{2}$; c, *B. fraxineum*, habit, $\times \frac{1}{4}$; d-f, *B. fragile*: d, habit, $\times \frac{1}{4}$; e, rachis and pinna base, $\times 6$; f, rhizome scales, $\times 13$.

glabrous, adaxially sulcate and yellowish brown, abaxially terete and yellowish brown to castaneous or atropurpureous; segments numerous, narrowly triangular, falcate or subfalcate, joined at or near the rachis by a narrow, usually acute sinus (or rarely a few basal ones free), the proximal 6-12 pairs gradually and conspicuously reduced, margins entire, plane or slightly revolute; veins distinct abaxially, indistinct to obscure adaxially, simple, or 1-forked at base, terminating near the margin, their tips abruptly enlarged. Fertile leaves pinnate, 20-50 cm. long, 4-8 (12) cm. broad; petiole 3-15 cm. long, yellowish to reddish brown (often darker abaxially), often with a few vestigial pinnae near base of lamina; lamina lanceolate to deltoid-ovate, gradually tapering to a caudate apical segment, reduced abruptly at base; rachis stramineous to light brown, often darker abaxially than adaxially; pinnae glabrous, linear, greatly constricted, larger ones 3-6 cm. long, 0.05-0.18 cm. broad, sessile, adnate and often slightly dilated to decurrent at base; indusium very narrow, entire.

This is doubtfully distinct from *B. binervatum* (Poir.) Morton & Lell. (West Indies) and *B. kunthianum* C. Chr. (South America). From *B. fragile* the former is supposed to differ in its concolorous rhizome scales, and the latter in its greater size. A comparison of all available neotropical collections with the appropriate types will very likely show them to be conspecific.

In Guatemala, *B. fragile* is also closely related to *B. ensiforme*, under which see further discussion.

Blechnum fraxineum Willd. Sp. Pl. 5: 413. 1810. *B. longifolium* Willd. loc. cit. *B. gracile* Kaulf. Enum. Fil. 158. 1824. *B. fraxinifolium* Desv. Prodr. 284. 1827. *B. intermedium* Link, Hort. Reg. Bot. Berol. 2: 75. 1833. *B. antillanum* Proctor, Brit. Fern Gaz. 9: 214. 1965.

In forests, thickets, and shaded ravines, often on wet stream or river banks, 75-1,000 m.; Alta Verapaz; Izabal; Petén; Retalhuleu; San Marcos; Suchitepéquez; Zacapa. Southern Mexico to Panama; West Indies; Colombia to the Guianas; south to Argentina and Paraguay.

Plants terrestrial; rhizome slender to rather stout, often stoloniferous, erect or ascending, amply provided with lanceolate to ovate, lustrous, castaneous to blackish scales, these mostly appressed, 3-4 mm. long, often with a very narrow, lighter brown margin; leaves erect, monomorphic (although sterile ones sometimes with shorter petioles), 20-55 (60) cm. long, 5-15 cm. broad, long-petiolate; petiole 8-33 (-37) cm. long, terete, or flattened at base, sulcate adaxially, stramineous to yellowish brown (or darker at very base), amply provided at base with orange to castaneous lanceolate scales to 3 mm. long; lamina pinnate, firm-herbaceous to chartaceous, glabrous, oblong-deltoid to ovate, broadest at or near the scarcely reduced base, terminating abruptly in an elongated, conform apical segment, this commonly free, longer than the lateral pinnae, and usually $\frac{1}{2}$ - $\frac{3}{4}$ the length of the lamina; rachis stramineous to yellowish brown, glabrous; pinnae 1-7 (9) pairs, ascending, linear to elliptic- or oblong-lanceolate, acute at apex, sessile to short-stalked, the base cuneate to rounded or cordate, if adnate then usually strongly to slightly narrowed (only rarely dilated) at the rachis, mostly falcate, the margins subentire and essentially plane; veins 1- or 2-forked, indistinct abaxially, obscure adaxially, terminating near the margin in enlarged, conspicuous tips; indusium

attached 0.2-0.8 mm. from the costa, persistent but sometimes irregularly lacerate at maturity, the margin subentire to erose, frequently undulate.

This is closely allied with *B. occidentale* (under which see further discussion). Its lamina is variable enough to have prompted earlier authors to maintain a number of "distinct" species within the complex, throughout the neotropics. Such differences include size, shape, and number of pinnae, shape of pinna base, or habit slender or robust. These variations appear to be infinite and inconsistent and do not necessarily conform with patterns of distribution or type of habitat. Even among Guatemalan collections, pinnae may be linear or broadly lanceolate, sessile or short-stalked, with bases very narrowly cuneate to broadly rounded or cordate, or even adnate; apical segments may be completely free, or variously adnate to the uppermost pinna. Even separation of the species into varieties would require purely arbitrary measures. *Blechnum antillanum*, the most recently described species, is said to differ from *B. fraxineum* and *B. longifolium* "in numerous details." Unfortunately, none of these features is elucidated, and I find this no more different from *B. fraxineum* than are all the others.

Blechnum lehmannii Hieron. Bot. Jahrb. Syst. 34: 473. 1904.
Struthiopteris maxonii Broadh. Bull. Torrey Bot. Club 39: 268. 1912.
B. maxonii (Broadh.) C. Chr. Index Fil. Suppl. 16. 1913.

In wet forests, on slopes and banks of ravines, 1,600-2,400 m.; Baja Verapaz; Chimaltenango; Jalapa; Zacapa. Mexico (Chiapas); Honduras; El Salvador to Colombia and Venezuela.

Plants terrestrial; rhizome ascending to erect, commonly becoming an epigeous caudex, to 40 cm. long and 1.5 cm. thick, sparsely to amply scaly, the scales 3-5 mm. long, castaneous to blackish brown, concolorous, mostly flaccid, lanceolate to ovate, the margins subentire; leaves subfasciculate at the rhizome apex, short-petiolate, dimorphous. Sterile leaves deeply pinnatisect, 20-45 cm. long, 3-8 (-9) cm. broad; petiole 3-10 cm. long, wiry to stout, stramineous to yellowish brown (rarely castaneous or atropurpureous), angular or flattened, glabrous or sparsely scaly, lacking vestigial, scalelike pinnae distant from the lamina base; lamina essentially glabrous, elliptical, tapering gradually but conspicuously at both ends, texture chartaceous to subcoriaceous; rachis stramineous to yellowish brown, terete and slightly to strongly prominulous abaxially, sulcate adaxially; segments 14-24 pairs, triangular to oblong, commonly falcate, obtuse to subacute (rarely acute), the larger ones 2-3 times as long as broad, joined at or near the rachis by a narrow, usually acute sinus, the proximal 4-5 (-7) pairs gradually and conspicuously reduced, with those nearest the base subauriculiform or lunate and often 3-4 times broader than long, margins entire, plane to slightly revolute; veins indistinct to obscure, simple or (more commonly) 1-forked slightly to well above the base, terminating just short of the margin, their tips abruptly dilated and discolored. Fertile leaves pinnate, 20-45 cm. long, 3.5-7 cm. broad; petiole 10-22 cm. long, stramineous to castaneous, often provided with vestigial, scalelike pinnae distant from the lamina base; lamina

narrow-elliptic or lanceolate, gradually or abruptly reduced at apex, rather abruptly reduced at base; rachis stramineous to gray-brown or (sometimes) castaneous; pinnae glabrous, linear, greatly constricted, larger ones 25-65 mm. long, 1.6-3 mm. broad, sessile, adnate, and slightly or not at all dilated at base; indusium quite narrow, entire to erose.

With this probably should be included *B. mexiae* Copel. of South America. An isotype at Field Museum shows little difference; however, I have seen no other material on which to base a decision. Significantly, Copeland's original description (Univ. Calif. Publ. Bot. 17: 32. 1932) did not compare his new species with *B. lehmannii*, so evidently he was unfamiliar with it at the time. The Lesser Antillean *B. l'herminieri* (Bory) C. Chr. is another species in the complex which needs further comparison. It seems to be a perfect intermediate between *B. lehmannii* and *B. divergens*. None of these species are distinguished by really significant characteristics. Diagnostic features are based chiefly on relative size or on characters which probably develop due to increase in size of the lamina.

***Blechnum occidentale* L. Sp. Pl. 1077. 1753 (as *B. orientale*; corrected in ed. 2: 1534. 1763).**

Plants terrestrial (rarely epipetric); rhizome slender to rather stout, often stoloniferous, erect or ascending, amply provided with lanceolate to ovate, castaneous to blackish scales, these mostly appressed, 2-4 mm. long, often with a narrow, lighter brown margin; leaves essentially monomorphous, 15-70 cm. long, (3) 5-18 cm. broad, long-petiolate; petiole (5) 8-34 cm. long, nearly equaling the lamina, terete, or flattened at base, sulcate adaxially, stramineous to light brown (or darker at very base), amply provided at base with orange to castaneous, lanceolate scales 3-5 mm. long; lamina pinnate to (distally) deeply pinnatisect, firm-herbaceous to chartaceous or subcoriaceous, glabrous, lanceolate to narrowly deltoid, broadest at or near the scarcely reduced base, gradually reduced to a pinnatifid or subcaudate apex; rachis stramineous to yellowish brown, glabrous, or sparsely to densely pubescent abaxially, the trichomes minute, spreading, pluricellular, and occasionally gland-tipped; pinnae 12-26 pairs, proximal ones not or scarcely reduced (or basal ones rarely $\frac{1}{2}$ as long as the largest central ones), spreading to ascending, falcate or subfalcate, acute to obtuse at apex, sessile to subsessile, or 2-3 proximal pairs short-stalked, the base cordate, or adnate and often strongly dilated, the margins subentire and essentially plane; veins 1- or 2-forked, indistinct or obscure, terminating near the margin, the tips scarcely to (more often) strongly enlarged; indusium attached 0.2-1 mm. from the costa and frequently decurrent onto the rachis, persistent, the margin subentire to erose.

Blechnum occidentale is very closely related to *B. fraxineum*. In fact the two differ in little more than the number of pinnae and the configuration of the leaf apex. In *B. occidentale* many pinnae are dilated at the broadly adnate base, whereas in *B. fraxineum* pinna bases are slightly narrowed and cordate, or at least not conspicuously dilated, but this feature is not particularly constant. The younger, sterile

leaves of *B. fraxineum* are sometimes nearly identical with those of *B. occidentale*.

Two varieties are recognized in Guatemala, the only apparent difference being the presence or absence of glandular, septate trichomes on the rachis abaxially. However, at least in Guatemala, this character correlates almost perfectly with altitudinal range. The typical, glabrous plants are found at 1,000 m. and below, the pubescent variety (var. *pubirhachis*) occurs from 1,200-2,700 m. Of all material examined from Guatemala a single glabrous collection has been reported above 1,200 m., and this a juvenile plant (*Steyermark 33776*, Quezaltenango). David Lellinger, U.S. National Herbarium, has advised (*pers. comm.*) that there is a similar correlation between varieties among specimens he has studied from Costa Rica and Panama.

***Blechnum occidentale* var. *occidentale*.** *B. caudatum* Cav. Descr. Pl. 262. 1802. *B. falciculatum* Presl, Epim. Bot. 106. 1849 (type from Jalapa, Mexico, *Galeotti 6397*).

In forests, thickets, and shaded ravines, often on wet stream banks, 50-1,000 (1,300) m.; Chimaltenango; Izabal; Quezaltenango; Retalhuleu; San Marcos; Santa Rosa; Zacapa. West Indies; Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Rachis and costae completely glabrous on both sides.

Blechnum occidentale* var. *pubirhachis Rosenst. Hedwigia 46: 94. 1906.

In forests, thickets, and shaded ravines, usually on steep banks, occasionally on rocks or rocky hillsides, 1,200-2,700 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Suchitepéquez. West Indies; Mexico; Honduras to Panama; Colombia and Venezuela, south to Brazil and Bolivia.

Rachis (and sometimes bases of costae) sparsely to densely pubescent abaxially, the trichomes spreading, minute, 0.1-0.5 mm. long, orange to castaneous, most of them gland-tipped, septate, composed of 2-6 cells.

Blechnum polypodioides Raddi, Opusc. Sci. 3: 294. 1819 (not [Sw.] Kuhn. 1868). *Asplenium blechnoides* Lag. in Sw. Syn. Fil. 76. 1806. *B. unilaterale* Sw. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 4: 79. 1810. *nom. superfl.* (an illegitimate change of epithet). *B. confluens* Schlecht. & Cham. in Linnaea 5: 613. 1830. *B. scabrum* Liebm. Kongel. Danske. Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 236

(seors. 84). 1849. *B. angustifrons* Fée Mém. Fam. Foug. 7: 25. 1857. *B. blechnoides* (Lag.) C. Chr. Index Fil. 151. 1905 (not Keys, 1873).

In forests and wooded ravines, on clay or rocky banks, often on banks of streams, rarely on mossy rocks, 300-1,400 m.; Alta Verapaz; Chiquimula; Huehuetenango; San Marcos; Santa Rosa; Zacapa. Mexico to Panama; Greater Antilles; Colombia; Venezuela; Brazil; Peru; Bolivia; Paraguay.

Plants terrestrial; rhizome slender, erect or ascending, amply provided with linear to lanceolate, lustrous, castaneous to blackish scales, these mostly appressed, 1-2 mm. long, often with very narrow, lighter brown margins, or those at the apex ferruginous; leaves erect, monomorphic, 8-46 (-60) cm. long, 1.6-8 cm. broad, short-petiolate; petiole 0.5-15 cm. long, terete, or flattened at base, sulcate adaxially, stramineous (or dark brown at the very base), amply provided (especially at base) with orange to light-brown, linear to ovate scales 2-5 cm. long, these often with lustrous, castaneous median strips or patches; lamina very deeply pinnatisect (or fully pinnate at base), firm-herbaceous to chartaceous, glabrous, slender, narrow-elliptic, broadest at or near the middle, tapering gradually to a pinnatifid apex, reduced gradually and conspicuously at base; rachis stramineous, glabrous, or minutely pubescent abaxially, prominulous and terete abaxially, sulcate adaxially; pinnae (or segments) 15-40 pairs, spreading at a broad (often 90°) angle from the rachis, narrow-deltoid, acute at the apex, adnate and often strongly dilated and auriculate at base, many of them subfalcate, the margins entire or very minutely serrulate, proximally becoming gradually and conspicuously shorter and more obtuse, with the lowermost 1-3 pairs often reduced to mere auricles, the larger, middle ones 1-4 cm. long and (beyond the dilated base) 0.2-0.8 cm. broad; sori often short and single on some pinnae (borne either on the acroscopic or the basiscopic side of the costa), commonly lacking on the reduced, proximal pinnae; veins indistinct, 1- or 2-forked, the tips not or slightly enlarged, terminating just short of the margin; indusium firm, subentire, or (rarely) erose, attached 0.4-0.8 mm. from the costa, persistent and rarely splitting at maturity.

There have been numerous problems concerning the taxonomy and the nomenclature of this species. It should not be confused with *B. polypodioides* (Sw.) Kuhn, a synonym of *B. fragile* (Liebm.) Mort. & Lell., which is quite a different fern. (The nomenclature of the latter has been clarified by Morton & Lellinger in Amer. Fern J. 57: 68. 1967.) However it often *has* been confused with numerous neotropical species, some of which are included in the list of synonyms above. Furthermore, it may not be truly distinct from *B. asplenioides* Sw. or *B. delicatum* Maxon & Morton, both from South America. These are supposedly smaller plants with narrower, more strongly tapering laminae and shorter and broader segments. *Blechnum polypodioides* is a highly variable species, with segments rather long and narrow to nearly as broad as long, the proximal ones (few to many of them) being moderately to very strongly reduced. So it is questionable whether the characteristics supposedly distinguishing these South American species are truly efficacious. If all species in the complex were to be

lumped together, *B. asplenioides* (1817) would have clear priority over all other names.

Blechnum schiedeana (Presl) Hieron. *Hedwigia* 47: 239. 1908. *Lomaria schiedeana* Presl, Tent. Pterid. 143. 1836. *L. longifolia* Schlecht. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 49. 1842. *L. spectabilis* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 235 (seors. 83). 1849. *Struthiopteris schiedeana* (Presl) Broadh. Bull. Torrey Bot. Club 39: 370. 1912.

In wet forests, thickets, and ravines, occasionally in wet clearings or at edges of swamps, 900-2,000 m.; Alta Verapaz; Guatemala; San Marcos; Zacapa. Southern Mexico; Honduras, El Salvador.

Plants terrestrial; rhizome slender to stout, erect, this and the petiole base amply provided with lanceolate, attenuate, flaccid scales, these orange to dark brown, 0.7-2 cm. long, 0.15-0.4 cm. broad; leaves erect, fully pinnate, to 1.7 m. long and 0.4 m. broad, dimorphous, long petiolate; petiole to 75 cm. long, stramineous to light brown, occasionally dark brown at base, the scales above the base sparse and often fugacious, these linear or linear-lanceolate, to 2 cm. long, flaccid, tawny to dark brown and often intermixed with minute orange scurf; lamina lanceolate or elliptic-lanceolate, chartaceous to subcoriaceous, not or scarcely reduced at base, gradually reduced at apex and terminating in a free, conform apical segment; rachis stramineous or yellowish brown, abaxially with a conspicuous, fusiform, (usually) dark-brown aerophore at the base of each pinna, sparsely to amply scurfy and scaly. Sterile pinnae 14-21 pairs, larger ones 10-22 cm. long, 1.5-2.8 cm. broad (on occasional specimens intermixed with partly or wholly fertile ones), linear-lanceolate, falcate to nearly straight, acuminate at apex, most short-stalked, tapered to broadly rounded at base, the margins slightly to strongly revolute, entire, but serrate at apex, glabrous, or the veins sometimes with a few scattered, minute scales abaxially; costae abaxially stramineous, strongly prominulous, naked to sparsely scaly or fibrillose, adaxially glabrous or essentially so, sulcate, or at least appearing so because of the parallel, raised, often cartilaginous ridges flanking it on either side; veins simple or 1-forked, terminating at pinna margin, abaxially distinct, somewhat prominulous, adaxially indistinct, the tips not or slightly enlarged and discolored. Fertile pinnae sessile to short-stalked, larger ones 10-18 cm. long, 0.2-0.4 cm. broad, the base tapered to rounded or cordate; costa glabrous, or sparsely scaly abaxially; indusium light or dark brown, subentire to strongly erose, often deeply lacerated.

Hieronymus (1908) mentions *B. schiedeana* as occurring in Ecuador and Colombia, but I have not see the specimens on which he based his opinion. However, this and *B. costaricense* may be conspecific with other South American taxa. See treatment of the latter for further discussion.

Blechnum serrulatum L. C. Rich. in Actes Soc. Hist. Nat. Paris 1: 114. 1792. *B. indicum* of authors (not Burm. 1768). *B. angustifolium* Willd. Sp. Pl. 5: 414. 1810.

In swamps, marshes, and along river banks, usually in savannas or in clearings, occasionally in thickets, sea level to 100 m.; Izabal; Petén.

Florida; West Indies; Mexico to Panama; Colombia to the Guianas, south to Argentina and Brazil.

Plants terrestrial, rhizome stout, creeping, bearing clusters of leaves on its erect or ascending branches, and provided with subappressed, linear to lanceolate scales, these 2-3 mm. long, dull brown or grayish brown, but often bicolorous, with a lustrous, dark-brown to blackish median stripe; leaves rigid, erect, monomorphous or essentially so, 55-100 cm. long, 8-24 cm. broad, the fertile ones with pinnae not or only slightly constricted; petiole dull yellowish or grayish brown, or darker at base, stout, terete abaxially, shallowly canaliculate adaxially, 15-55 cm. long, equaling to $\frac{1}{4}$ as long as the lamina, glabrous, but amply scaly at the very base; lamina 30-50 cm. long, 8-24 cm. broad, pinnate, oblong or lanceolate, slightly reduced at base, terminating abruptly in a conform or subconform apical segment, coriaceous or subcoriaceous, sparsely and minutely scaly on the axes abaxially; rachis free throughout; pinnae numerous, strongly ascending, subsessile to short-stalked, conspicuously articulate at the rachis, linear to oblong-lanceolate, acute, 3-15 cm. long, 0.5-1.8 cm. broad, the margins sharply and conspicuously serrate; veins distinct, crowded, commonly 1-forked near the costa, tips not enlarged, terminating at the margin; sori borne on all pinnae throughout the fertile lamina, or as often only on the more distal ones; indusium with margins erose, deeply lacerate at maturity, and then often becoming fragmented, attached 0.2-0.4 mm. from the costa.

Blechnum stoloniferum (Fourn.) Mett. ex C. Chr. Index Fil. 160. 1905. *Lomaria stolonifera* Fourn. Mex. Pl. 1: 113. 1872. *L. ghiesbreghtii* Bak. in Hook. & Bak. Syn. Fil. ed. 2: 481. 1874. *B. ghiesbreghtii* (Bak.) C. Chr. Index Fil. 154. 1905. *Struthiopteris stolonifera* (Fourn.) Broadh. Bull. Torrey Bot. Club 39: 277. 1912.

In wet forests, on steep banks, ledges, or on the forest floor, 2,400-3,300 m., Chimaltenango; San Marcos; Totonicapán. Mexico.

Plants terrestrial; rhizome short-creeping to ascending, rarely more than 1 cm. thick, stoloniferous, amply scaly, the scales 3-6 mm. long, light to dark brown, concolorous, rather flaccid, lanceolate to ovate, with margins entire; leaves subfasciculate, very short-petiolate, dimorphous. Sterile leaves deeply pinnatisect, (in ours) 6-20 cm. long and 1.5-3.2 cm. broad; petiole 0.5-5 cm. long, wiry, castaneous to atropurpureous, angular or flattened, glabrous or with a few, scattered scales, lacking vestigial, scalelike pinnae distant from the lamina base; lamina essentially glabrous, narrow-elliptic, tapering gradually but conspicuously at both ends, texture thin- to firm-herbaceous; rachis stramineous to yellow- or gray-brown (rarely castaneous at base), terete and slightly to strongly prominulous abaxially, sulcate adaxially; segments 12-24 pairs, triangular to oblong, straight to subfalcate, obtuse (or rarely appearing acute due to the revolute margins), larger ones commonly 1.5-2 times as long as broad, joined at or near the rachis by a narrow, usually acute sinus (or rarely a few basal ones free), the proximal 6-12 pairs gradually and conspicuously reduced; veins indistinct to obscure, simple, or 1-forked well above the base, terminating near the margin, their tips often abruptly enlarged. Fertile leaves pinnate or deeply pinnatisect, 12-24 cm. long, 1.2-2.2 cm. broad; petiole 2.2-6 cm. long, castaneous to atropurpureous; lamina linear to narrow-elliptic, gradually or abruptly reduced at apex, gradually and conspicuously reduced at base, occasionally with the basal few pairs of pinnae sterile; rachis stramineous to gray-brown, or castan-

eous toward the base; pinnae (or segments) glabrous, linear, greatly constricted, larger ones 8-15 mm. long, 1.2-2.7 mm. broad, sessile, adnate to strongly decurrent at base; indusium quite narrow, entire to erose.

BOLBITIS Schott

REFERENCES: C. Christensen, On the American species of *Lep-tochilus* sect. *Bolbitis*, Bot. Tidsskr. 26: 283-297. 1904. K. Iwatsuki, Taxonomic studies of Pteridophyta IV: Emendation of *Bolbitis* . . . Acta Phytotax. Geobot. 18: 44-59. 1959. E. Hennipman, A monograph of the fern genus *Bolbitis*, Leiden Univ. Press (Leiden Bot. Ser. 2). 1977.

Plants terrestrial or epiphytic; rhizome woody, creeping or scandent, lacking trichomes, but amply to densely scaly, the scales commonly dark brown and clathrate; leaves dimorphous, commonly less than 1.5 m. long, approximate to remote (rarely crowded), sparsely scaly, but lacking trichomes; petiole not articulate, sparsely scaly, terete abaxially, canaliculate adaxially; lamina simple and entire to (in ours) pinnate to pinnate-pinnatifid, the fertile ones similar but narrower and with pinnae and/or lobes considerably smaller; rachis canaliculate, with several ridges adaxially, these often raised and winglike; pinnae continuous or (in a few species) articulate on the rachis, the costa or margin decurrent onto a wing or ridge on the rachis; veins free, or (in ours) copiously reticulate, the areoles with (in ours) or without free, included veinlets; fertile laminae or their divisions contracted, the abaxial surface covered with sporangia, indusia and paraphyses lacking; spores monolete, globose or subglobose, with perine.

Opinions vary as to proper delimitation of this genus, the principal question being whether to include or exclude the 10 or 12 free-veined Asian species of *Egenolfia*. Iwatsuki (1959) held that venation is the only significant character distinguishing the latter from *Bolbitis*, and hence insufficient grounds for separating the two. The genus so circumscribed is pantropical, consisting of about 44 species (according to Hennipman, 1977), with the greatest number occurring in the Old World.

- a. Lamina gradually reduced to a pinnatifid apex. *B. portoricensis*.
- a. Lamina with a conform or subconform terminal "pinna" (this rarely with a basal lobe).
 - b. Pinnae numerous, with margins serrate to crenate, sterile ones 1.5-3 cm. broad; included free veinlets seldom many, these directed toward the margin.
B. bernoullii.
 - b. Pinnae 1-4 pairs, entire (or rarely broadly sinuate), sterile ones 4-12 cm. broad; included free veinlets many, the tips spreading in all directions.
 - c. Lamina firm-herbaceous, the ultimate venation distinct; apical "pinna" 6.5-10 cm. broad; petiole of sterile leaf slightly to considerably shorter than the lamina. . .
B. nicotianaefolia.
 - c. Lamina chartaceous, the ultimate venation commonly obscure or indistinct; apical "pinna" 12-17 cm. broad; petiole of sterile leaf longer than the lamina.
B. pergametacea.

Bolbitis bernoullii (Kuhn ex Christ) Ching, in C. Chr. Index Fil. Suppl. 3: 47. 1934. *Acrostichum bernoullii* Kuhn ex Christ, Bull. Soc. Roy. Bot. Belgique 35 (1): 244. 1896 (type "entre Escamillas et Palohucco, Costa Grande de Guatemala," *Bernoulli & Cario 382*). *Gymnopteris bernoullii* (Kuhn ex Christ) Diels, Nat. Pflanz. 1 (4): 201. 1899. *Leptochilus bernoullii* (Kuhn ex Christ) Bot. Tidsskr. 26: 296. 1904. *Gymnopteris donnell-smithii* Christ, Bull. Herb. Boissier II. 6: 290. 1906 (type from Cubilguitz, Alta Verapaz, *Tuerckheim s.n.* ed. Donn.-Sm. 8830). *G. tuerckheimii* Christ, *loc. cit.* (type from Cubilguitz, Alta Verapaz, *Tuerckheim s.n.* ed. Donn.-Sm. 8831). *Poikilopteris donnell-smithii* (Christ) Maxon, Contr. U.S. Natl. Herb. 13: 20. 1909. *Leptochilus donnell-smithii* (Christ) C. Chr. Index Fil. Suppl. 48: 1913. *L. tuerckheimii* (Christ) C. Chr. *loc.cit.* *Bolbitis donnell-smithii* (Christ) Ching, in C. Chr. Index Fil. Suppl. 3: 48. 1934.

In dense, wet forests, creeping along the ground or climbing tree trunks, 50-1,500 m.; Alta Verapaz; Izabal; Petén; Quezaltenango; San Marcos. Southern Mexico; British Honduras; Honduras.

Plants terrestrial or epiphytic; rhizome stout, creeping, amply to densely provided with lustrous, dark-brown, thick, rigid, lanceolate scales, these with elongated cells and spinulose-dentate margins; leaves remote or (in scandent plants) often crowded and obliquely ascending near rhizome tip, to about 1 m. long. Sterile leaf 21-38 cm. broad; petiole 16-30 cm. long (much shorter than the lamina), stramineous or yellowish brown, scaly at base as on the rhizome, becoming scattered and linear above; lamina pinnate, herbaceous, lanceolate, ovate, or subdeltoid, tapering abruptly with a conform or subconform terminal "pinna" (this rarely with 1 basal lobe), lacking a proliferous bud, the rachis, costae, and costules glabrous or provided with a few, scattered, dark-brown, linear to hairlike scales; pinnae lanceolate, 10-many pairs, the larger ones 14-18 cm. long and 2-3 cm. broad, short-stalked, articulated (sometimes indistinctly) at the rachis, cuneate to broadly rounded at base, crenate or remotely serrate, acuminate at apex; veins raised and distinct, primary ones 5-8 mm. apart, transverse ones arcuate and often bearing 1 or 2 free veinlets which are always directed toward the margin. Fertile leaf 14-20 cm. broad; petiole 14-30 cm. long ($\frac{1}{2}$ - $\frac{1}{2}$ the length of the lamina); pinnae (larger, fully fertile ones) 6-12 cm. long and 0.5-0.9 cm. broad, lanceolate or linear-lanceolate, subacute, entire.

Bolbitis nicotianaefolia (Sw.) Alston, Kew Bull. 1932: 310. 1932. *Acrostichum nicotianaefolium* Sw. Syn. Fil. 13: 199. 1806. *A. acuminatum* Willd. Sp. Pl. 5: 116. 1810. *Gymnopteris acuminata* (Willd.) Presl, Tent. Pterid. 244. 1836. *Leptochilus nicotianaefolius* (Sw.) C. Chr. Bot. Tidsskr. 26: 285. 1904.

In wet forests and thickets, often along streams and in ravines, 75-1,400 m.; Alta Verapaz; Huehuetenango; Izabal; Quezaltenango. Honduras; Costa Rica; Panama; West Indies; the Guianas; Colombia; Ecuador; Peru.



FIG. 14. *Bolbitis*. a, *B. portoricensis*, habit, $\times \frac{1}{2}$; b-c, *B. bernoullii*: b, habit (silhouette), $\times \frac{1}{2}$; c, portion of pinna, showing venation, $\times 5$; d, *B. nicotianaefolia*, portion of pinna, showing venation, $\times 5$.

Plants (in our area) terrestrial; rhizome stout, creeping, amply provided with reddish- or dark-brown, slightly lustrous, thick, lanceolate scales, these subentire or remotely ciliate, with isodiametric or elongated cells; leaves subdistant, to nearly 1 m. long. Sterile leaf 20-40 cm. broad; petiole 20-35 cm. long (considerably shorter than the lamina), yellowish brown or stramineous, scaly at base as on the rhizome, but also provided above with thin, amorphous, appressed scales, and scattered, spreading, linear to filamentous, tortuous ones; lamina pinnate, firm-herbaceous, subdeltoid, terminating in an apical segment similar to the pinnae, lacking a proliferous bud, the rachis and costae provided abaxially with scattered, minute, dark-brown, filamentous squamulae; pinnae 1-4 pairs, 15-30 cm. long, 4-8 cm. broad, lanceolate, straight, and essentially equilateral, cuneate (often broadly so) at base, entire or broadly and irregularly sinuate, acuminate, the apical "pinna" similar though slightly larger; principal veins oblique, about 1 cm. apart, slightly arcuate, prominent or becoming indistinct and crooked toward the margin, transverse veins slightly arcuate, enclosing copious areoles which in turn enclose usually 1-2 free veinlets, the tips spreading in all directions, the ultimate venation prominulous and usually distinct. Fertile leaf 9-12 cm. broad; petiole 35-50 cm. long (always longer than the lamina); pinnae 4-10 cm. long, 1.2-2 cm. broad, lanceolate, obtuse to acute, entire.

This and *B. pergamentacea* are closely related. However, some additional characters besides those noted in the key may be used to separate the two. Pinnae of *B. pergamentacea* often are relatively much broader, many of them subfalcate and asymmetrical in the proximal half, *e.g.*, the basiscopic side broader and cuneate at a much wider angle, and the principal veins are strongly elevated and quite distinct nearly to the margin. Pinnae of *B. nicotianaefolia* are usually more elongated, essentially straight, and equilateral, and the principal veins are less strongly elevated and often become somewhat indistinct and crooked toward the margin.

Two interesting collections from Quezaltenango should be noted—*Standley 86748* (US), *Steyermark 33411* (F)—which may represent a new species or may be merely aberrant specimens of *B. nicotianaefolia*. In both, the lamina is subtripartite (*i.e.*, consisting of a greatly elongated apical section, bearing at its base a pair of strongly ascending pinnae, each about one-third its size) and the principal veins are rather indistinct, running not in a straight line toward the margin, but instead irregularly forked and crooked. Both specimens consist of two sterile leaves, and were collected about a year apart in what may be the same location: a wet quebrada near Patzulín, about 1,200-1,400 m. No other collections of *B. nicotianaefolia* have been made in Guatemala above 300 m., so these specimens may represent merely ecological variants.

Bolbitis pergamentacea (Maxon) Ching, in C. Chr. Index Fil. Suppl. 3: 49. 1934. *Leptochilus pergamentaceus* Maxon, J. Wash. Acad. Sci. 14: 144. 1924.

In wet forests, often along rivers and streams; 50-500 m.; Alta Verapaz; Petén. Mexico (Chiapas); Honduras to Panama; Greater Antilles; Venezuela; Colombia.

Plants terrestrial; rhizome stout, creeping, amply provided with orange or reddish brown, slightly lustrous, thick, lanceolate to ovate scales, these subentire, with isodiametric or slightly elongated cells; leaves subdistant, to 1.2 m. long. Sterile leaf 25-35 cm. broad; petiole 40-70 cm. long (always longer than the lamina), gray- or yellow-brown, scaly at base as on the rhizome, but also provided above with very thin, amorphous, appressed scales and some spreading, linear to filamentous, tortuous ones; lamina pinnate, chartaceous, subdeltoid, terminating in an apical segment very similar to (though often broader than) the pinnae, lacking a proliferous bud, the rachis and costae provided abaxially with scattered, minute, dark-brown, filamentous squamulae; pinnae 1-3 pairs, 20-30 cm. long and 6-10 cm. broad, ovate, subfalcate, sessile or short-stalked, cuneate at the often asymmetrical base, entire, long-acuminate, the apical "pinna" similar, but 12-17 cm. broad; principal veins oblique, about 1 cm. apart, slightly arcuate, very prominent nearly to the margin, transverse veins strongly arcuate, enclosing copious areoles which in turn commonly enclose 1-2 free veinlets, the tips spreading in all directions, the ultimate venation indistinct or obscure. Fertile leaf 12-14 cm. broad; petiole 65-75 cm. long (much longer than the lamina); pinnae 7-12 cm. long, 1.5-2.5 cm. broad, lanceolate, obtuse to acute, entire.

This is closely related to *B. nicotianaefolia*, under which see further discussion.

Bolbitis portoricensis (Sprengel) Hennisman, Amer. Fern J. 65: 30. 1975. *Acrostichum portoricense* (Sprengel), Nov. Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 10: 226. 1821. *A. cladorrhizans* Sprengel, *tom. cit.* 225. *Gymnopteris portoricensis* (Sprengel) Fée, Hist. Acrost. 85. 1845. *Anapausia portoricensis* (Sprengel) Presl, Epim. Bot. 188. 1849. *Poecilopteris lobulosa* Presl, *tom. cit.* 174. *Lep-tochilus cladorrhizans* (Sprengel) Maxon, Pterid. Porto Rico 460. 1926. *B. cladorrhizans* (Sprengel) Ching, in C. Chr. Index Fil. Suppl. III: 47. 1934.

In forests or thickets, often in ravines, 50-1,900 m.; Escuintla; Guatemala; Huehuetenango; Izabal; Petén; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Suchitepéquez. Mexico; British Honduras; Honduras to Colombia and Venezuela; Ecuador; West Indies.

Plants terrestrial; rhizome stout, creeping, amply provided with lustrous, dark-brown, thick, rigid, lanceolate scales, these with elongated cells and subentire, or sometimes slightly erose or very sparsely ciliate near the base; leaves densely crowded, 0.8-1 m. long. Sterile leaf 30-50 cm. broad; petiole 40-60 cm. long (nearly as long as the lamina), stramineous to light- or yellow-brown, scaly at base as on the rhizome, but provided above with very thin, amorphous, tightly appressed scales; lamina pinnate, thin-herbaceous, subdeltoid, tapering gradually to a pinnatifid apex, often long-attenuate and bearing a proliferous bud on the upper rachis and/or at the flagelliform tip, the rachis, costae, and costules provided abaxially with scattered, dark-brown, ovate to

linear, long-acuminate scales; pinnae 4-8 pairs below the pinnatifid apical section, mostly 12-24 cm. long and 2-5 cm. broad, sessile or (lower ones) short-stalked, rounded to cuneate at base, crenate to lobed, acuminate at apex, most of them essentially symmetrical but lower ones strongly asymmetrical (these basiscopically enlarged and more deeply lobed); veins distinct, areoles with free included veinlets, tips of the latter diverging in all directions. Fertile leaf 18-22 cm. broad; petiole 50-75 cm. long (much longer than the lamina); pinnae 5-15 cm. long and 0.6-1.4 cm. broad, linear or narrow-lanceolate, subacute or obtuse, entire to sinuate or lobed.

This should be confused with no other species of *Bolbitis* in Guatemala, as it is the only one with a nonconform apical section. *Bolbitis aliena* (Sw.) Alston, of the Greater Antilles and South America, is found as far north as Honduras and is very similar, but lacks free included veinlets.

BOMMERIA Fournier

REFERENCE: W. R. Maxon, Notes upon *Bommeria* and related genera, Contr. U.S. Natl. Herb. 17: 168-171. 1913.

Plants small, terrestrial or epipetric; rhizome slender, short- or long-creeping, scaly, the scales thin and orange to light brown, or thick, rigid, and dark-brown to blackish; leaves monomorphous, crowded to subdistant; petiole long, sparsely pubescent, or often densely so and scaly at base, not articulate; lamina pubescent, firm-herbaceous to subcoriaceous, commonly much shorter than the petiole, pedate, deltoid to pentagonal, pinnatifid to 2-pinnatifid (or sometimes 3-pinnatifid as to enlarged basal pinnae), gradually to abruptly tapering to a pinnatifid apex; rachis pubescent, free (if at all) only to above the basal pinnae; primary segments few, the basal pair much the largest (often nearly as large as the rest of the lamina, and then the lamina appearing subtrifoliate), these strongly inequilateral at base, more strongly produced basiscopically; venation free and branching (in ours), or areolate, and then the areoles lacking free included veinlets; sporangia short-stalked, borne abaxially along the veins (often only toward the segment margin), not arranged in discrete sori; indusia lacking (but sporangia partly protected by the reflexed segment margin in *B. ehrenbergiana*); paraphyses lacking; spores trilete, globose-tetrahedral, with perine.

This is very closely related to *Gymnopteris* and *Hemionitis*, and it may be that eventually all will be considered congeneric (see treatments of the latter two for further discussion). *Bommeria* contains five Mexican species, one of which is found also in the southwestern United States, and the following, which occurs also in Guatemala, Honduras, and Nicaragua.

Bommeria pedata (Sw.) Fourn. Bull. Soc. Bot. France 27: 327. 1880. *Hemionitis pedata* Sw. Syn. Fil. 20: 209. 1806. *Gymnogramma pedata* (Sw.) Kaulf. Enum. Fil. 69. 1824. *Neurogramma pedata* (Sw.) Link, Fil. Hort. Berol. 139. 1841. *Gymnopteris pedata* (Sw.) C. Chr. Index Fil. 341, 1905.



FIG. 15. *Bommeria pedata*. a, habit, $\times \frac{1}{2}$; b, pinna apex, abaxial surface, $\times 6$; c, pinna apex, adaxial surface, $\times 6$.

In forests, wooded ravines, or clearings, on rocks or on the forest floor, often in dry or sandy soil, 1,300-2,000 m.; Alta Verapaz; Baja Verapaz; Guatemala; Huehuetenango; Jalapa; Sacatepéquez; Santa Rosa; Sololá. Mexico; Honduras; Nicaragua.

Rhizome abundantly scaly, the scales 3-5 mm. long, varying from orange, rather thin and flaccid, and lanceolate or lance-ovate, to blackish, thick and rigid, and linear or linear-lanceolate, or often bicolorous (orange, with a dark median stripe); leaves several, crowded, 12-32 cm. long; petiole terete or subterete, lustrous, castaneous to atropurpureous, glabrous, or sparsely pubescent or scaly at the base; lamina 4-9 cm. long, 4-12 cm. broad, often as broad as or broader than long and usually much shorter than the petiole, pinnatifid to 2-pinnatifid (or 3-pinnatifid as to enlarged basal pinnae), deltoid or pentagonal, often appearing 3-foliate (as the basal pinnae are sometimes nearly as large as the rest of the lamina), chartaceous to subcoriaceous, sparsely to amply strigose adaxially and on the margin, densely pilose abaxially; rachis prominulous and amply pilose abaxially, immersed and subglabrous adaxially; primary segments mostly subentire, broadly adnate, proximal ones becoming deeply lobed, basal ones deeply pinnatifid (occasionally 2-pinnatifid) and nearly as large as the rest of the lamina, markedly inequilateral at their base, the basiscopic segments much more strongly produced and more deeply lobed; veins free, several-forked, the clavate tips extending to the margin.

This may be separated from all but one species of *Bommeria* by the venation, which is free throughout the lamina. The only other free-veined species, *B. hispida*, has smaller leaves with pubescence so abundant that the abaxial surface is often completely obscured. Furthermore, the rachis (and often the costae) are amply provided on the abaxial side with pale, lanceolate scales. The only scales on *B. pedata* are found on the rhizome and the base of the petiole.

CERATOPTERIS Brongniart

REFERENCES: R. C. Benedict, The genus *Ceratopteris*: a preliminary revision, Bull. Torrey Bot. Club 36: 463-476. 1909; and *Ceratopteris*, in No. Amer. Fl. 16: 29-30. 1909. R. M. Lloyd, Systematics of the genus *Ceratopteris* Brongn. (Parkeriaceae) II, Taxonomy, Brittonia 26: 139-160. 1974.

Plants aquatic or semiaquatic, rooted or floating; rhizome reduced, horizontal to ascending or trailing, sparsely scaly, the scales broad, flaccid, light to dark brown; roots borne on the petiole at or near the base; petiole not articulate, soft-herbaceous, often inflated, flattened in drying, sparsely scaly, the scales light brown, broad, flaccid, appressed, often circular or reniform; leaves crowded, dimorphous, glabrous, soft-herbaceous, sterile ones with broad segments, fertile ones more highly dissected, with narrower, constricted segments. Sterile leaves with lamina simple (palmately or pinnately lobed) to 3-pinnate, decompound ones tapering to a broad, pinnatifid apex, often provided with proliferous buds in the axils of pinnae or sinuses of segments; rachis green, glabrous, but sometimes sparsely scaly as on the petiole, soft-herbaceous, flattened in drying; pinnae or lobes 1-8 pairs, ascending, opposite or alternate; venation

reticulate, the areoles without free, included veinlets. Fertile leaves 3- to 5-pinnate (at least in the proximal half); pinnae 5-12 pairs, finely dissected, larger than the sterile ones; ultimate segments linear, acute, inrolled to enclose several rows of sporangia; sporangia borne abaxially along the longitudinal veins, not arranged in discrete sori, globose, thin-walled, very short-stalked (appearing sessile), the annulus longitudinal, sometimes vestigial, sometimes interrupted distally as well as at the stalk, and bearing 0 to many indurate cells; indusia none; spores 16 to 32 to a sporangium, trilete, tetrahedral, strongly ridged, with very thin perine.

I follow the treatments of Bower and Christensen in placing *Ceratopteris* within the Polypodiaceae, among the Gymnogrammoid ferns. Although the sporangia appear sessile, they are actually borne on very minute stalks. The annulus is highly variable, often crooked, sometimes vestigial, sometimes interrupted distally. However, it is essentially longitudinal and interrupted proximally at the point of attachment, just as in other genera of the Polypodiaceae (*sens. lat.*). The genus frequently has been placed in a family by itself, recognized either as Parkeriaceae or Ceratopteridaceae. For those wishing to adopt this classification, the former name has priority.

The lamina in the following treatment, as in others before mine, is described as "pinnate" to "5-pinnate," but these terms must be taken in a very loose sense. The petiole and other axes of the leaf are herbaceous, with the tissue virtually undifferentiated and continuous from the axes onto all the various segments. Therefore it probably would be more accurate to consider the leaves "pinnatifid" to "5-pinnatifid." Leaves in *Ceratopteris* are highly variable in size, shape, and dissection, so it is not hard to understand why the taxonomy has long been so confused. Lloyd recognizes four species in his recent revision (1974)—three of these from Guatemala—and I follow his treatment closely. As the laminae and most of the other features of *Ceratopteris* are so variable, there is great difficulty in delineating species. The only really constant character is the 16 (*vs.* 32) spores per sporangium in *C. richardii*. Therefore with many specimens, the following key can only be effective when utilizing the full combination of characters employed.

The genus is represented in tropical and subtropical regions of both the New and the Old World.

- a. Basal pinnae (or midveins of segments) borne oppositely on the rachis; sterile lamina commonly palmately or pinnately lobed (basal pair occasionally pinnate-pinnatifid); sporangia with annulus cells usually few to 10, or lacking; spores 32 per sporangium. *C. pteridoides*.
- a. Basal pinnae borne alternately on the rachis; sterile lamina pinnate-pinnatifid to 3-pinnate; sporangia with annulus cells usually 13-70; spores 16 or 32 per sporangium.
 - b. Sporangium containing 32 spores; sterile lamina pinnate-pinnatifid to 3-pinnate, fertile ones 3- to 4-pinnate. *C. thalictroides*.

- b. Sporangium containing 16 spores; sterile lamina pinnate-pinnatifid to 2-pinnate, fertile ones 4- to 5-pinnate. *C. richardii*.

Ceratopteris pteridoides (Hook.) Hieron. Bot. Jahrb. Syst. 34: 561. 1905. *Parkeria pteridoides* Hook. Exot. Fl. 2: 1825. *P. lockhartii* Hook. & Grev. Icon. Fil. t. 97. 1828. *C. parkeri* J. Sm. J. Bot. (London) 4: 70. 1841. *nom. superfl.* *C. lockhartii* (Hook. & Grev.) Kunze, Linnaea 23: 241. 1850.

In ponds, or in slow-moving rivers or streams, sea level to 100 m.; Izabal; Petén. El Salvador to Panama; Colombia to French Guiana, south to Peru and Argentina; Greater Antilles; Florida; Louisiana.

Plants floating, occasionally rooted in mud. Sterile leaves deltoid, rhomboid, or ovate, often cordate, 8-30 cm. long, 6-24 cm. broad, palmately to pinnately lobed (or occasionally pinnate-pinnatifid at the very base), the lobes commonly obtuse to subacute, often bearing proliferous buds in their sinuses; lamina commonly with 1-2 pairs of pinnae (or lobes); basal segments (or pinnae) or midveins of basal lobes borne oppositely on the rachis. Fertile leaves deltoid, cordate, or reniform, 15-50 cm. long, 10-35 cm. broad; lamina 3- to 4-pinnate (at least in the proximal half); pinnae 4-9 pairs, ascending, basal pair often opposite; sporangia with annulus lacking or vestigial, the indurated cells 0-12 (-40); spores 32 to each sporangium.

Ceratopteris pteridoides apparently hybridizes readily with other species, especially in Central America. Lloyd (1974) cites a number of specimens from Mexico, El Salvador, Costa Rica, and Panama in which this species has formed hybrids with *C. richardii*. However, all collections I have seen from Guatemala appear to be typical.

Ceratopteris richardii Brongn. Dict. Class. Hist. Nat. 3: 351. 1823. *C. deltoidea* Benedict, Bull. Torrey Bot. Club 36: 472. 1909.

Apparently represented in Guatemala by a single collection, by an unknown collector, marked simply "Guatemala, 27 Mai 1876" (the specimen at U.S. National Museum, a duplicate from the Paris Museum); otherwise found in ditches, rivers, marshes, and ponds, sea level to 350 m.; Louisiana; Greater Antilles; Venezuela to French Guiana and Brazil; Africa.

Plants rooted, occasionally floating. Sterile leaves lanceolate to deltoid, 8-45 cm. long, 3-24 cm. broad, pinnate-pinnatifid to 2-pinnate, often bearing buds (mostly dormant) in the axils of pinnae or sinuses of lobes; lamina with 4-6 pairs of pinnae, the basal pair commonly alternate on the rachis. Fertile leaves lanceolate to deltoid, 15-85 cm. long, 5-30 cm. broad; lamina 4- to 5-pinnate (at least in the proximal half); pinnae 5-8 pairs, ascending, deeply dissected, basal pair commonly alternate; ultimate segments widely spreading, linear and acute; sporangia with annulus of many (15-65) indurated cells; spores 16 to each sporangium.

Macroscopically, this and *C. thalictroides* are virtually impossible to



FIG. 16. *Ceratopteris*. a, *C. pteridoides*, habit, $\times \frac{1}{2}$; b-d, *C. thalictroides*: b, habit, $\times \frac{1}{2}$; c, portion of fertile pinna, showing inrolled margins and sporangia, $\times 7$; d, sinus of sterile pinna lobes, showing proliferous bud, $\times 7$.

separate, except that the latter often has somewhat less dissected fertile laminae and more highly dissected sterile laminae. According to Lloyd's treatment (1974) the only consistent difference is the number of spores in each sporangium.

Ceratopteris thalictroides (L.) Brongn. Bull. Sci. Soc. Philom. Paris ser. 3, 8: 186. 1821. *Acrostichum thalictroides* L. Sp. Pl. 1070. 1753.

In lakes and ponds, in swamps, water-filled ditches, and slow-moving streams, 0-75 m.; Escuintla; Izabal; Santa Rosa. Florida; Greater Antilles; southern Mexico to Panama; Colombia; Venezuela; Surinam; Ecuador; Brazil; Old World tropics and subtropics.

Plants rooted, occasionally floating. Sterile leaves lanceolate to deltoid, sometimes cordate, 6-60 cm. long, 2-20 cm. broad, pinnate-pinnatifid to 3-pinnate, often bearing buds (mostly dormant) in the axils of pinnae or sinuses of lobes; lamina with 2-5 pairs of pinnae, the basal pair commonly alternate on the rachis. Fertile leaves lanceolate to deltoid, often cordate, 10-100 cm. long, 4-40 cm. broad; lamina 3- to 4-pinnate (at least in the proximal half); pinnae 6-10 pairs, ascending, deeply dissected, basal pair commonly alternate; ultimate segments widely spreading, linear and acute; sporangia with annulus of many (20-70) indurated cells; spores 32 to each sporangium.

CHEILANTHES Swartz

Plants terrestrial or epipetric; rhizome short-creeping to ascending or erect, scaly; leaves essentially monomorphic, short- to long-petiolate, of small to moderate size; petiole not articulate, terete, scaly, pubescent, or glabrous, castaneous, atropurpureous or blackish (rarely lighter colored); lamina pinnately divided (1- to 4-pinnate) or, rarely, with pinnae all radiating from the apex of the petiole, gradually tapering to a pinnatifid apex, or terminating in a discrete, conform apical segment, scaly, pubescent, or glabrous, or occasionally white- to yellow-farinose; rachis terete, or adaxially flattened or sulcate, scaly, pubescent or glabrous; pinnae several to numerous, subequilateral, or in some species the basal pair inequilateral (much more strongly produced basiscopically at base); ultimate segments highly variable, broad-ovate or circular to linear, plane to strongly revolute, or greatly constricted and beadlike; veins free, forked, commonly much thickened at the tips; indusium continuous or interrupted, consisting of the strongly revolute or reflexed segment margin which is usually greatly modified (lighter in color and thinner in texture), or if not greatly modified then the entire segment beadlike and protectively folded in over the sporangia; sporangia stalked, borne at the tips of veins; paraphyses lacking; spores (in ours) trilete, tetrahedral or globose-tetrahedral, with perine.

Copeland, in his *Genera Filicum* (1947), describes this as a "difficult and unsatisfactory genus." If anything, this is an understatement. As with trains in a busy rail terminal, species seem to arrive and depart from *Cheilanthes* with astonishing regularity. Various authors have added to it, or subtracted from it, species of such genera as *Adiantopsis*, *Cheiloplecton*, *Doryopteris*, *Mildella*, *Notholaena*, and *Pellaea*.

Those species which occur in certain, relatively small geographical areas may appear to fit satisfactorily into one or more of these generic categories. But anyone who examines large numbers of species throughout, for example, the neotropics discovers that the features traditionally used to delimit these genera vary so widely as to be quite undependable. Such features are: lamina farinose or not; lamina glabrous, or pubescent, or scaly; fertile segment margins strongly *vs.* scarcely revolute; fertile margins not, or strongly, modified as to color and/or texture; indusia (fertile margins) continuous or interrupted. The type of key used in this Flora to separate *Cheilanthes*, *Notholaena*, and *Pellaea* is, just like those used by previous authors, based on combinations of the above characters. Furthermore, in these keys it has been necessary to employ modifying phrases in order to include or exclude the marginal species—such as *Notholaena sulphurea*, *Pellaea formosa*, *P. rigida*, *P. skinneri*.

In recent years, excellent studies have been published dealing with various parts of the problem, *i.e.*, according to small, individual genera, sections of larger genera, or genera as occurring in certain geographic areas. These have helped to (1) more sharply define many species, (2) solidly establish some relationships and species concepts, and (3) prepare the way for more definitive studies. The most important task remains—to pool all the data in one comprehensive study, a problem so complex that it might be performed best by a team of specialists. It would appear that the ultimate solution will be either to lump all species into one large genus or to divide them among a dozen smaller ones.

Cheilanthes, as recognized here, contains about 120 species, occurring in temperate and tropical areas of both hemispheres. Many thrive in exposed, xeric habitats. The following have been found in Guatemala.

- a. Lamina yellow- or white-farinose abaxially.
 - b. Lamina yellow-farinose and pubescent with white, septate trichomes; rhizome scales broad, thin-textured, tawny. *C. aurea*.
 - b. Lamina white-farinose, otherwise glabrous; rhizome scales linear or lanceolate, rigid, partially sclerotic, castaneous to blackish. *C. farinosa*.
- a. Lamina not farinose.
 - c. Lamina with (3) 5-9 branches all radiating from the same point at apex of petiole. *C. radiata*.
 - c. Lamina with branches pinnately arranged along the rachis.
 - d. Rachis scaly or rather long-pubescent; abaxial side of segments scaly or pubescent (in 2 species sometimes sparsely so or glabrate).
 - e. Ultimate segments abundantly provided abaxially with ovate-attenuate scales, these often obscuring the tissue. *C. myriophylla*.

- e. Ultimate segments pubescent, or sometimes glabrate, not scaly (a few hairlike scales may be present on costae or costules).
- f. Lamina subpentagonal, often nearly as broad as long; basal pinnae inequilateral at base, much more strongly produced basiscopically; petiole 2.5-4 times as long as the lamina. *C. kaulfussii*.
- f. Lamina linear-lanceolate to narrow-deltoid, obviously longer than broad; basal (and other) pinnae subequilateral; petiole shorter than or equaling (or rarely somewhat longer than) the lamina.
- g. Ultimate segments beadlike, amply to copiously covered with long, tortuous, spreading, persistent trichomes; lamina 3-pinnate to nearly 4-pinnate. *C. lendigera*.
- g. Ultimate segments not beadlike, amply provided abaxially with short, subappressed trichomes, or glabrate; lamina 2-pinnate to nearly 3-pinnate.
- h. Pinnules (especially abaxially) amply provided with minute, pale yellow or whitish, 1- to 2-celled, curved or appressed trichomes; mature indusia irregular and interrupted, commonly erose or erose-ciliate.
C. microphylla.
- h. Pinnules essentially glabrous, or provided abaxially with a few orange or light-brown, long, spreading trichomes; mature indusia either elongated and subentire or narrow and cucullate with an entire or erose margin.
- i. Pinnules subentire or with a basal acroscopic auricle; rhizome rather stout, erect to ascending (rarely short-creeping), the leaves crowded to subcaespitose. *C. notholaenoides*.
- i. Pinnules cut deeply to the costule into 2-4 pairs of segments or lobes; rhizome slender, rather long-creeping, the leaves approximate to subdistant. *C. cucullans*.
- d. Rachis glabrous; abaxial side of segments glabrous (in a few species appearing pubescent due to densely ciliate indusia).
- j. Indusium borne the length of the segment, conspicuously decurrent as a broad wing along the segment stalk and often onto the next axis below.
- k. Indusium subentire or minutely and regularly denticulate.
C. chaerophylla.
- k. Indusium conspicuously erose and fimbriate.
- l. Ultimate segments of fertile leaves elliptic, obovate or spatulate (rarely linear), 1.5-2 (3) times as long as broad, seldom glandular-spinulose or -pustulose. *C. marginata*.
- l. Ultimate segments of fertile leaves commonly linear, (3) 4-10 times as long as broad, glandular-spinulose or -pustulose adaxially (especially near the margin). *C. pyramidalis* v. *pyramidalis*.
- j. Indusium usually not extending the full length of the segment, not decurrent along the segment stalk.
- m. Indusia long and continuous along each segment margin; petiole sulcate adaxially, the broad ridges neither light colored nor herbaceous; pinnules obliquely ascending.
- n. Veins indistinct or obscure, not prominent; rhizome scales 3-6 mm. long, linear or lanceolate, mostly with a thin, light-colored margin; ultimate segments abaxially often lightly dotted with red glands.
C. pyramidalis v. *arizonica*.

- n. Veins distinct and prominulous (especially abaxially); rhizome scales 2-3 mm. long, linear or subulate, concolorous; ultimate segments never with red glands. *C. angustifolia*.
 m. Indusia commonly short and discrete, terminal on the lobes of ultimate segments; petiole not sulcate, but adaxially flattened toward the lamina, with a thin, light-colored, usually herbaceous, ridge running up each side; pinnules mostly spreading at right angles. *C. chlorophylla*.

Cheilanthes angustifolia H. B. K. Nov. Gen. et Sp. Pl. 1: 21. 1815.

C. cuneata Link, Hort. Reg. Bot. Berol. 2: 40. 1833. *C. angustifolia beta cuneata* (Link) Moore, Index Fil. 234. 1861. *Pellaea angustifolia* Bak. in Hook. & Bak. Syn. Fil. 150. 1867. *P. angustifolia beta cuneata* (J. Sm.) Bak. loc. cit. *P. angustifolia* var. *elongata* Rov. Pterid. Sur. Mex. 130. 1909. *Cheilanthes angustifolia* var. *cuneata* Brause, Verh. Bot. Vereins. Prov. Brandenburg 51: 5. 1910.

In forests and wooded ravines, on dry banks, slopes, or ridges, 1,200-2,000 m.; Chiquimula; Huehuetenango; Quezaltenango: El Quiché; Santa Rosa; Sololá; Zacapa. Mexico; Honduras; El Salvador; Nicaragua to Colombia and Venezuela.

Plants terrestrial (in Guatemala) or often epipetric; rhizome horizontal to ascending or erect, provided with linear or subulate, lustrous, castaneous to blackish scales, these 2-3 mm. long; leaves crowded, 10-40 cm. long, 3-12 cm. broad, long-petiolate, petiole 5-20 cm. long, as long as or longer than the lamina, sublustrous, atropurpureous, essentially glabrous, terete abaxially, sulcate adaxially, the ridges neither light colored nor herbaceous; lamina 2-pinnate to 3-pinnate-pinnatifid, elongate-triangular, firm-herbaceous to chartaceous, glabrous; rachis terete abaxially, sulcate adaxially, the ridges flanking the groove broadly rounded and herbaceous, these continuing as similar ridges along the costae; pinnae 8-14 pairs, alternate, at least the proximal ones stalked, ascending (often strongly so), the basal ones somewhat inequilateral (more strongly produced basiscopically); pinnules rather strongly ascending; ultimate segments highly variable, linear or narrow-elliptic and 8-10 times longer than broad to ovate or obovate and 2-3 times longer than broad; veins distinct, rather strongly prominulous (especially abaxially); indusia reflexed, strongly modified (often scarious), entire to erose, often undulate, neither ciliate nor fimbriate, commonly long and continuous or rarely (on immature plants) short and interrupted, borne along each margin of the ultimate segment from tip to a point somewhat above the base, never decurrent along the base and onto the segment stalk.

The variability of dissection in the lamina and shape of ultimate segments has prompted a number of authors to treat this as two different species or as several varieties. In leaves where the lamina is merely bipinnate or bipinnate-pinnatifid, the ultimate segments tend to be narrow and very elongated. But in laminae which are tripinnate-pinnatifid (as to basal pinnae), the ultimate segments are commonly rather broad, and ovate to obovate. Thus two plants superficially may appear quite different, although close examination will reveal them to be essentially the same in all other features. Between



FIG. 17. *Cheilanthes*. a, *C. kaulfussii*, habit, $\times \frac{1}{2}$; b, *C. lendigera*, pinnule with ultimate segments, $\times 12$; c, *C. farinosa*, pinnules, $\times 6$; d, *C. angustifolia*, pinnule, $\times 6$; e, *C. chaerophylla*, apex of pinna, $\times 6$.

the two extremes one can find an uninterrupted series of gradations, any of which defy circumscription, nor do any particular variants seem to conform to certain geographic boundaries.

Cheilanthes aurea Baker in Hook. & Bak. Syn. Fil. 453. 1868.

Rare, on banks of ravines or rivers, 900-1,000 m.; Chiquimula; Zacapa (type from Motagua [as "Montagua"], *Salvin & Godman, s.n.* 1862). Mexico; El Salvador.

Plants terrestrial; rhizome short, erect, amply provided with tawny, lanceolate or ovate scales, these 3-4 mm. long, thin, minutely but obviously clathrate, entire; leaves several to numerous, caespitose, 7-15 cm. long, 4-8 cm. broad, petiolate; petiole 3.5-8 cm. long, equaling or somewhat shorter than the lamina, slightly lustrous, castaneous, subterete to flattened, shallow-sulcate adaxially, sparsely yellow-farinose, amply septate-pubescent and (at least toward base) scaly as on the rhizome; lamina pinnate-bipinnatifid (or more highly dissected as to the enlarged basal pinnae), thin- to firm-herbaceous, deltoid or subpentagonal, tapering gradually to a pinnatifid apex, sparsely to amply pubescent on both sides, the trichomes white and septate, the abaxial surface yellow-farinose, the farina not completely obscuring the tissue; rachis castaneous, somewhat lustrous, amply to abundantly septate-pubescent, and sometimes also with a few tawny scales, sulcate adaxially, the parallel ridges (above lamina base) provided with green tissue, thus the rachis gradually becoming alate distally; pinnae 6-10 pairs, subopposite, all but the lower ones sessile and adnate, pinnatifid to 2-pinnatifid (or basal ones 3-pinnatifid), the basal pair conspicuously inequilateral, much more strongly produced basiscopically, costae alate throughout; ultimate segments broadly rounded, entire, crenate, or shallowly lobed; veins indistinct or obscure, commonly 1-forked; indusium broad, scarious, glabrous, subentire or undulate.

Cheilanthes chaerophylla (Mart. & Gal.) Kunze, *Linnaea* 23: 243 & 307. 1850. *Allosorus chaerophyllus* Mart. & Gal. *Nouv. Mém. Acad. Roy. Sci. Bruxelles* 15: 47. 1842.

In forests and wooded ravines, on rocks or on rocky, clay banks, 2,800-3,900 m.; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez; Sololá; Totonicapán; Zacapa. Mexico; Honduras; El Salvador; Nicaragua?; Costa Rica.

Plants commonly epipetric; rhizome erect or ascending, provided with linear or linear-lanceolate, lustrous scales, these 2-3 mm. long, castaneous to blackish, often with a very narrow, lighter colored margin; leaves numerous, caespitose, 12-48 cm. long, 3-12 cm. broad, long-petiolate; petiole 8-32 cm. long, commonly much longer than the lamina, lustrous, light brown to castaneous (rarely atropurpureous), essentially glabrous, but at base (especially in ours) often with a few spreading, brown scales to 8 mm. long, terete abaxially, shallow-sulcate adaxially, the ridges neither light colored nor herbaceous; lamina 3-pinnate-pinnatifid to nearly 4-pinnate, deltoid to subpentagonal, firm-herbaceous to chartaceous, glabrous; rachis terete abaxially, sulcate adaxially, the ridges (especially distally) flanking the groove broadly rounded and herbaceous, these continuing as similar ridges onto costae and costules; pinnae 6-10 pairs, commonly imbricate, alternate or the proximal ones subopposite, short-stalked, ascending (but not strongly

so), the basal ones inequilateral, much more strongly produced basiscopically; pinnules (at least larger ones) short-stalked, crowded to imbricate, the costule green-alate; ultimate segments obtuse, elliptic, obovate or spatulate, 1.5-2 times as long as broad; veins indistinct or obscure, not prominulous; indusium strongly reflexed and modified, very broad, often touching or overlapping that of the opposite margin, decurrent onto the segment stalk and often along the axis below, margin frequently undulate, subentire or (more often) minutely and regularly denticulate.

Guatemalan plants of this species seem to differ slightly from Mexican and Honduran specimens I have seen. The latter usually have atropurpureous petioles, which are adaxially grooved only at the apex. Petioles of *C. chaerophylla* from Guatemala typically are brown and are adaxially sulcate nearly their full length.

Cheilanthes chlorophylla Sw. Kongl. Vetensk. Acad. Handl. 76. 1817. *Adiantopsis chlorophylla* (Sw.) Fée, Mém. Fam. Foug. V. (Gen. Fil.): 145. 1852.

Apparently known in Central America from only two Guatemalan collections: *Salvin & Godman 33*, from Alotenango, Sacatepéquez (ca. 1,400 m.); and *Steyermark 37965*, on forested slopes of Volcán Tajumulco along Río Cabús, alt. 1,300-1,500 m. Otherwise known only from South America: Brazil; Ecuador; Peru; Bolivia; Paraguay; Argentina.

Plants terrestrial or epipetric; rhizome short-creeping to erect, provided with linear-lanceolate to subulate scales, these 3-4 mm. long, castaneous to blackish, with very narrow, light-brown margins; leaves crowded, 20-80 cm. long, 10-25 cm. broad, long-petiolate; petiole 12-35 cm. long, about as long as the lamina, lustrous, castaneous to atropurpureous, glabrous or with a few, scattered, castaneous trichomes, essentially terete, but toward the lamina adaxially flattened and with light-colored, usually herbaceous ridges on each side; lamina ovate to elongate-triangular, 2-pinnate-pinnatifid to 3-pinnate-pinnatifid, firm-herbaceous to chartaceous, leaf tissue and axes essentially glabrous; rachis adaxially flattened, with 2 very thin, widely separated, herbaceous ridges which are usually continuous as wings along the costae and costules; pinnae well spaced, numerous, stalked, subequilateral, elongate-triangular, with 10-18 pairs of sessile or subsessile, spreading, subdistant pinnules; ultimate segments adnate, oblong or broadly elliptic, subentire or lobed, the margins plane to somewhat reflexed; veins obscure or indistinct, not prominulous, commonly simple or 1-forked; indusia several on each segment margin, usually discrete (rarely merging and thus appearing nearly continuous), consisting of reflexed, strongly modified (often scarious) marginal lobes.

This has been included by some authors in the genus *Adiantopsis* along with *C. radiata*, under which see further discussion.

Cheilanthes cucullans Fée, Mém. Fam. Foug. 7: 39, t. 25, f. 4. 1857.

Apparently known from Guatemala by a single collection (*Hatch & Wilson 329*, dry bank of Río Panajachel, Dept. Sololá), otherwise confined to Mexico, on rocks or rocky banks of ravines.

Plants commonly epipetric; rhizome rather long-creeping and slender, provided with linear-lanceolate, attenuate scales, these 2-3 mm. long, orange or bicolorous, with a blackish median stripe; leaves approximate to subdistant, 10-35 cm. long, 2.5-7 cm. broad, petiolate; petiole 4-18 cm. long, equaling or shorter than the lamina, terete, lustrous, atropurpureous to blackish, sparsely to densely provided with tawny to orange, arachnoid trichomes, these often intermixed with orange to whitish, filamentous scales; lamina 2-pinnate-pinnatifid to nearly 3-pinnate (rarely fully 3-pinnate as to the bases of the largest pinnae), elliptic-lanceolate to elongate-triangular, firm-herbaceous, slightly or not at all reduced at base, gradually tapered to a pinnatifid apex; rachis terete, abundantly scaly and pubescent as on the petiole; pinnae alternate, spreading or ascending, oblong-lanceolate or narrow-triangular, costae amply provided with long, orange trichomes and whitish to orange, filamentous scales, atropurpureous to blackish abaxially, greenish except at base; pinnules cut deeply (rarely quite) to the costule into 2-4 pairs of obtuse lobes or segments, glabrous adaxially, sparsely provided along the costule abaxially with scattered, orange or light-brown, arachnoid trichomes, or glabrate; fertile ultimate segments strongly revolute; indusia formed by the somewhat to strongly modified, subentire or erose segment margin, narrow and cucullate on the larger segment lobes but rather long and continuous along the elongated, undissected pinnule apices.

This and *C. notholaenoides* might better be recognized as varieties of *C. microphylla* (under which see further discussion). But such a decision should be held in abeyance pending revision of the entire species complex.

***Cheilanthes farinosa* (Forsk.) Kaulf. Enum. Fil. 212. 1824. *Pteris farinosa* Forsk. Fl. Aegypt.-Arab. 187. 1775.**

In open forests, thickets, and ravines, on rocks or crevices of cliffs or sometimes on clay banks, 1,200-3,700 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; El Quiché; Sacatepéquez; San Marcos. Mexico; Colombia to Peru; Old World.

Plants commonly epipetric; rhizome small to stout, decumbent to erect, amply provided with rigid, linear or lanceolate, castaneous to blackish or faintly bicolorous scales, these 5-8 mm. long, attenuate, partially sclerotic, entire; leaves numerous, subcaespitose, 10-60 cm. long, 3-14 cm. broad, petiolate; petiole 5-30 cm. long, about as long as or longer than the lamina, lustrous, castaneous to atropurpureous, terete, glabrous, with a few scales near the base; lamina pinnate-pinnatifid to pinnate-bipinnatifid, firm-herbaceous to chartaceous, narrowly to broadly deltoid, tapering gradually to a pinnatifid apex, essentially glabrous, but abaxially white-farinose, the farina often so dense as to obscure the tissue; rachis lustrous, castaneous to atropurpureous, neither paleaceous nor pubescent, sulcate adaxially, the ridges concolorous with the rachis, but distally becoming green-alate; pinnae 8-18 pairs, subopposite, all but the lower ones sessile and adnate, the basal pair conspicuously inequilateral, strongly produced basiscopically, pinnatifid to bipinnatifid, cut nearly to the costa into 6-10 pairs of obtuse, crenate to pinnatifid segments, the costae alate throughout; veins indistinct to obscure, commonly 1-forked; indusium very broad, pale brown to scarious, glabrous, crispate, essentially continuous.

Cheilanthes kaulfussii Kunze, *Linnaea* 13: 145. 1839. *C. viscosa* Link, Hort. Reg. Bot. Berol. 2: 43. 1833 (not Carm. 1818).

In forests and wooded ravines, less often in open or lightly shaded locations, commonly on rocks and in crevices of rocky cliffs, or sometimes on rocky hillsides; 900-3,300 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Jalapa; Jutiapa; Sololá. Texas; Mexico; Honduras; El Salvador; Nicaragua; Costa Rica.

Plants commonly epipetric; rhizome horizontal to ascending, or erect, provided with subulate, lustrous, castaneous to blackish scales, these 2-4 mm. long; leaves crowded, usually subfasciculate, 10-55 cm. long, 4-14 cm. broad, long-petiolate; petiole 8-40 cm. long, 2.5-4 times as long as the lamina, sublustrous, castaneous to atropurpureous, terete, abundantly glandular-puberulent; lamina short, subpentagonal, often nearly as broad as long, 3-pinnate or 3-pinnate-pinnatifid, firm-herbaceous to chartaceous, everywhere glandular-puberulent, or sometimes glabrate abaxially; rachis terete, or slightly flattened abaxially, castaneous to atropurpureous, abundantly puberulent; pinnae 8-10 pairs, subopposite or alternate, very short-stalked, at least the basal pair inequilateral, much more strongly produced basiscopically; ultimate segments obovate and entire, to obtusely ovate and pinnatifid at base, the margins slightly to strongly revolute; veins obscure; indusia discrete, 1 or several to each ultimate segment, consisting partly of the revolute segment margin and partly of a rather strongly modified (sometimes scarious) extension of the marginal lobe.

Cheilanthes lendigera (Cav.) Sw. Syn. Fil. 128. 1806. *Pteris lendigera* Cav. Descr. Pl. 268. 1802.

In forests and wooded ravines, sometimes in open areas, on rocks or in crevices of rocky cliffs, or on rocky or clay banks, 1,600-3,100 m.; Guatemala; Huehuetenango; El Progreso; Quezaltenango; San Marcos; Sololá; Totonicapán; Zacapa. Hispaniola; southwestern United States; Mexico; Nicaragua to Colombia and Venezuela.

Plants terrestrial to epipetric; rhizome slender, long-creeping, provided with linear-lanceolate, attenuate scales, these 2-3 mm. long, orange to ferruginous, or the older ones bicolorous, castaneous to blackish with a narrow, light-brown margin; leaves well-spaced on the rhizome, 10-45 cm. long, 2.5-12 cm. broad, petiolate; petiole 5-25 cm. long, commonly shorter than (rarely somewhat longer than) the lamina, terete, lustrous, castaneous to atropurpureous, glabrate, or sparsely to abundantly provided with a mixture of tawny or whitish hairlike scales and long (to 5 mm.), tortuous trichomes; lamina 3- to 4-pinnate, elliptic-lanceolate to narrow-deltoid, slightly or not reduced at base, tapering gradually to a pinnatifid apex; rachis terete, or slightly flattened adaxially, castaneous to atropurpureous, amply to abundantly villous and scaly as on the petiole; pinnae 12-20 pairs, alternate, short-stalked, spreading or weakly ascending, narrow-deltoid, subequilateral, axes and abaxial surface densely villous, glabrous on adaxial surface of segments; ultimate segments minute, circular to obovate, many of them convex-concave (thus appearing beadlike as viewed adaxially); veins obscure; sporangia few (2-6) to each ultimate segment; indusium consisting of a usually continuous, revolute segment margin which ultimately becomes strongly modified (commonly scarious) and often so broad that the opposing edges nearly meet beneath the segment.

Cheilanthes marginata H. B. K. Nov. Gen. et Sp. Pl. 1: 22. 1815.

In wooded ravines, forests, or clearings, on clay or rocky banks or slopes, or in rocky crevices, 2,400-4,000 m.; Chimaltenango; Huehuetenango; Quezaltenango; San Marcos; Sololá; Totonicapán. Mexico; El Salvador; Costa Rica; Colombia and Venezuela, south to Argentina.

Plants terrestrial or epipetric; rhizome short-creeping, ascending or erect, provided with lustrous brown to castaneous scales, these 3-5 mm. long, linear or lanceolate, attenuate, often with very narrow, lighter brown margins; leaves numerous, crowded to caespitose, 8-45 cm. long, 4-12 cm. broad, long-petiolate; petiole 6-30 cm. long, nearly equaling to (commonly) much longer than the lamina, sublustrous, brown to atropurpureous, essentially glabrous, terete abaxially, sulcate adaxially, the ridges neither light colored nor herbaceous; lamina 3- to 4-pinnate, deltoid to subpentagonal, firm-herbaceous to (rarely) chartaceous, glabrous; rachis terete abaxially, sulcate adaxially, the ridges (especially distally) flanking the groove broadly rounded and herbaceous, these continuous as similar ridges onto costae and costules; pinnae 6-10 pairs, commonly imbricate, sessile, or the basal pair short-stalked, somewhat ascending, the basal ones inequilateral, much more strongly produced basiscopically; pinnules (at least larger ones) short-stalked, crowded, or sometimes imbricate, the costule green-alate throughout; ultimate segments obtuse, those of fertile leaves elliptic, obovate, or spatulate, 1.5-2 (3) times as long as broad, adaxial tissue essentially smooth; veins indistinct or obscure, not prominulous; indusium strongly reflexed and modified, rather broad, but rarely touching that of the opposite segment margin, decurrent onto the segment stalk and often along the axis below, the margin frequently undulate, conspicuously glandular-fimbriate and erose.

Cheilanthes marginata belongs to a much confused and poorly studied complex of American species which includes, among others, *C. chaerophylla*, *C. cuneata*, *C. hirsuta* Link, *C. pyramidalis*, and *C. rufopunctata* Rosenst. In this group, laminae are essentially glabrous (no farina, simple trichomes or scales), ultimate segments are relatively broad or long (not beadlike), and indusia are continuous along the segment margin. Features which have been traditionally used to distinguish these taxa are dissection of lamina, shape of ultimate segments, occurrence of glands on the tissue, and type of indusia. Unfortunately most of these characters tend to be rather variable, and/or inconsistently linked with the others. If indusial characters are the best measure of species relationships, then *C. rufopunctata* and *C. pyramidalis* var. *arizonica* stand well apart from the rest, for their indusia are neither erose-fimbriate nor decurrent along the segment stalks. Also, in both, the segments often bear red glands abaxially. Interestingly the former is apparently confined to Peru and Bolivia, whereas the latter is found from Arizona to Honduras. Of the other five taxa, *C. chaerophylla* and *C. cuneata* (considered synonymous in this treatment) have subentire indusia, while indusia of *C. hirsuta*, *C. marginata*, and typical *C. pyramidalis* are conspicuously erose-

fimbriate. I have not seen the type of *C. hirsuta*, but from the description and type photograph I judge it to be the same as *C. marginata*. *Cheilanthes pyramidalis* perhaps might be best considered a variety of the latter. Unfortunately, these must remain merely presumptions, pending a thorough study of all the taxa, and their types, throughout their entire range.

Cheilanthes microphylla (Sw.) Sw. Syn. Fil. 127. 1806. *Adiantum microphyllum* Sw. Nov. Gen. Sp. Pl. Prodr. 135. 1788.

On rocks or in crevices of rocky cliffs, 600-1,200 m.; Alta Verapaz; Petén. Southeastern United States (Florida and coastal Alabama); West Indies; Mexico; British Honduras; Honduras; Colombia.

Plants commonly epipetric; rhizome short-creeping with leaves approximate or subdistant, or ascending to erect with leaves subcaespitose, provided with linear-lanceolate, attenuate scales, these 2-3 mm. long, tawny, orange, ferruginous, or bicolorous with a blackish median stripe; leaves 10-55 cm. long, 2.5-6 cm. broad, petiolate; petiole 4-20 cm. long, commonly about $\frac{1}{2}$ as long as the lamina, terete, lustrous, atropurpureous or blackish, occasionally glabrate, more commonly provided with orange, tawny, or whitish, usually appressed trichomes, these minute and with 2-3 cells, or long and arachnoid, with many cells; lamina 2-pinnate to nearly 3-pinnate (rarely fully 3-pinnate as to the base of largest pinnae), elliptic-lanceolate or elongate-triangular, firm-herbaceous, slightly or not at all reduced at base, gradually tapered to a pinnatifid apex; rachis terete, atropurpureous to blackish, amply to abundantly pubescent as on the petiole, the trichomes often intermixed with a few, filamentous scales; pinnae alternate, short-stalked, spreading or ascending, lance-ovate or narrow triangular, costae amply pubescent, blackish abaxially, greenish adaxially except at base; pinnules subentire with a pronounced acroscopic auricle, to nearly pinnate, but typically deeply pinnatifid with 1-3 pairs of lobes, amply puberulent abaxially, sparsely to amply so (or glabrate) adaxially, the trichomes minute, pale yellow or whitish, 1- to 2-celled, curved or appressed; fertile ultimate segments rather strongly revolute; indusium somewhat to strongly modified, commonly erose or erose-ciliate, irregular and interrupted (occasionally subentire and subcontinuous on young leaves).

With this probably should be included *C. cucullans* and *C. notholaenoides*, which do not appear to differ significantly. Both essentially lack the minute, appressed trichomes which are present on segments of *C. microphylla*. But other supposed diagnostic features are either overlapping or inconsistent. Rhizomes of *C. cucullans* are slender and creeping, with leaves rather well-spaced, whereas those of *C. notholaenoides* are typically stout and erect or ascending, with leaves subcaespitose. Rhizomes and spacing of leaves in *C. microphylla* tend to be intermediate between the two. A similar comparison may be made regarding dissection of pinnae. Typically, the pinnules of *C. notholaenoides* are subentire, or with a prominent acroscopic auricle, and those of *C. cucullans* deeply and regularly pinnatifid. Laminae in *C. microphylla* vary widely from the former condition to the latter.

Indusia in *C. notholaenoides* are commonly subentire and continuous. Those of *C. microphylla* are typically erose-ciliate and interrupted, but immature indusia are often indistinguishable from those of *C. notholaenoides*. The specific epithet of *C. cucullans* stems from the "hooded" appearance of the usually short and discrete indusial flaps of this species. But perhaps this is merely a by-product of the more dissected pinnules, for at the subentire tips of pinnules indusia may be continuous and similar to those of *C. notholaenoides*.

In certain parts of the range, characteristics appear to be rather stable, and identifications therefore are not so difficult (e.g., *C. notholaenoides* in South America, *C. microphylla* in the West Indies). It is in Mexico and Central America where most of the intermediate conditions occur. A thorough study is needed of the entire species complex (including *C. alabamensis* [Buckl.] Kunze of Mexico, and *C. moritziana* Kunze of South America) before its components may be finally and properly delimited.

While this *Flora* was in press, Alan Smith published his new var. *fimbriata* (Amer. Fern J. 70: 19. 1980), from southern Mexico. It is said to differ from the typical chiefly in the longer indusial trichomes. Two Guatemalan specimens were also cited.

***Cheilanthes myriophylla* Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 328. 1811.**

In forests or wooded ravines, on cliffs or rocks or on rocky hillsides, often in dry situations, 1,400-2,400 m.; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sololá. Hispaniola; Mexico; Honduras; Nicaragua; Colombia and Venezuela, south to Brazil and Argentina.

Plants terrestrial to epipetric; rhizome rather stout, erect or ascending, provided with lustrous, bicolorous, linear-lanceolate to filamentous scales, these 3-5 mm. long, castaneous to blackish and sclerotic, with narrow, lighter brown margins; leaves fasciculate, 12-35 cm. long, 2-4 cm. broad, petiolate; petiole 5-20 cm. long, commonly equaling or longer than the lamina, castaneous to atropurpureous, terete, this and the rachis abundantly provided with white, tawny, or brown scales, these subappressed, lanceolate to linear or filamentous; lamina 3- to 4-pinnate, chartaceous to subcoriaceous, narrow-lanceolate or oblanceolate, slightly or scarcely reduced at base, tapering gradually to a pinnatifid apex; rachis terete, castaneous to atropurpureous; pinnae 12-20 pairs, alternate, mostly short-stalked, narrow-deltoid, densely covered abaxially with white to brown, ovate-attenuate (often hair-tipped) scales, glabrous or sparsely pubescent adaxially; ultimate segments very small, beadlike, obovate to nearly circular in outline, actually almost orbicular because of the strongly revolute margins; veins completely obscured; sporangia few (2-6) to each ultimate segment, well protected by the nearly continuous, slightly or scarcely modified, revolute segment margin which serves as an indusium.

Cheilanthes notholaenoides (Desv.) Maxon ex Weath. Contr. Gray Herb. 114: 34. 1936. *Pteris notholaenoides* Desv. Mém. Soc. Linn. Paris 6: 298. 1827.

On rocks, rock outcrops, crevices of cliffs, or rocky hillsides, in shaded or exposed areas, 1,000-3,400 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; El Quiché; Sacatepéquez; Zacapa. Hispaniola; Mexico; Costa Rica; Colombia; Venezuela; Peru; Argentina.

Plants commonly epipetric; rhizome rather stout, erect or ascending (rarely short-creeping), leaves crowded to subcaespitose, provided with linear-lanceolate, attenuate scales, these 2-3 mm. long, orange, or bicolorous with a blackish median stripe; leaves 12-60 cm. long, 3-8 cm. broad, petiolate; petiole 5-23 cm. long, commonly much shorter than the lamina, terete, lustrous, atropurpureous or blackish, occasionally glabrate, more commonly provided with orange, tawny, or whitish, usually appressed trichomes, these minute, with 2-3 cells, or long and arachnoid, with many cells; lamina commonly 2-pinnate, (rarely 2-pinnate-pinnatifid), lanceolate to narrow-ovate, firm-herbaceous, slightly reduced at base, gradually tapered to a pinnatifid apex; rachis terete, atropurpureous to blackish, amply to abundantly pubescent as on the petiole, the trichomes often intermixed with a few filamentous scales; pinnae alternate, sessile or subsessile, spreading or ascending, oblong-lanceolate or narrow-triangular, costae amply pubescent, blackish abaxially, greenish adaxially except at base; pinnules subentire, but the larger ones commonly with a pronounced acroscopic auricle, glabrous, or occasionally very sparsely puberulent abaxially, fertile margins strongly revolute; indusium long and continuous, consisting of the subentire, revolute segment margin which is ultimately slightly modified and lighter colored.

It is with some reluctance that I maintain this as a distinct species. The characters traditionally separating it from *C. microphylla* are inconstant and not particularly significant, at least at species level. See discussion of the latter for further comparison.

Cheilanthes pyramidalis Fée, Mém. Fam. Foug. 7: 38, t. 25, f. 3. 1857.

Plants terrestrial or epipetric, rhizome short-creeping, ascending or erect, provided with lustrous, castaneous to blackish scales, these 3-6 mm. long, linear or lanceolate, attenuate, commonly with very narrow, lighter brown margins; leaves numerous, crowded to caespitose, 10-50 cm. long, 4-12 cm. broad, long-petiolate; petiole 8-40 cm. long, commonly much longer than the lamina; sublustrous, castaneous to atropurpureous or blackish, essentially glabrous, terete abaxially, sulcate adaxially, the ridges neither light-colored nor herbaceous; lamina 2- to 4-pinnate, narrow-deltoid to subpentagonal, firm-herbaceous to subcoriaceous, glabrous; rachis terete abaxially, sulcate adaxially, the ridges (especially distally) flanking the groove broadly rounded and herbaceous, these continuous as similar ridges onto costae and costules; pinnae 6-12 pairs, crowded to somewhat spaced, sessile, or the proximal ones short-stalked, somewhat ascending, the basal ones inequilateral, much more strongly produced basiscopically; pinnules sessile, or larger ones short-stalked, ascending, crowded; ultimate segments linear to obovate; veins indistinct or obscure; indusium continuous, strongly reflexed and modified, rather broad.

Two very distinct varieties are recognized in Guatemala. Indeed, var. *arizonica* might better be considered another species. Knobloch and Correll (1962) state that ". . . it might well be raised to specific rank since its combined differences from typical *C. pyramidalis* seem to be as strong, if not stronger, than some characteristics that are used to separate other species . . ." With this I heartily agree, but there currently exists such confusion among closely related taxa that this kind of reclassification should only be made within the context of a complete revision of the species complex. See discussion of *C. marginata* for further elaboration.

Cheilanthes pyramidalis var. **arizonica** (Maxon) Broun, Index No. Amer. Ferns 51. 1938. *C. pyramidalis* ssp. *arizonica* Maxon, Amer. Fern J. 8: 116. 1918.

In coniferous forests, on clay banks or rocky slopes, occasionally on rocks, 1,600-3,800 m.; Huehuetenango; El Quiché; Zacapa. Southwestern United States (Arizona); Mexico; Honduras.

Ultimate segments firm-herbaceous, elliptic, obovate, or spatulate (rarely linear), essentially smooth on the adaxial surface, frequently provided with red gland-dots on the abaxial surface and along the wings of the stalks; indusia borne along each margin of the ultimate segment from tip to a point somewhat above the base, never decurrent along the base and segment stalk, margin minutely glandular-papillose.

Although tentatively maintained herein as a variety of *C. pyramidalis*, this is much more closely allied to *C. rufopunctata* Rosenst. of Peru and Bolivia, which it resembles in its nondecurrent, eciliate indusia and the red glands which are frequently borne on the segments.

Cheilanthes pyramidalis var. **pyramidalis**.

In forests, thickets, or clearings, in soil or in crevices of rocky cliffs, 1,000-3,000 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; Jalapa; Quezaltenango; Sacatepéquez; San Marcos; Sololá; Totonicapán. Mexico; Honduras; El Salvador; Costa Rica; Panama; Colombia; Venezuela.

Ultimate segments chartaceous to subcoriaceous, most of them linear or narrowly oblong, often pendent, (3) 4-10 times as long as broad, glandular-spinulose or -pustulose (especially near the margin) adaxially, lacking red gland-dots; indusium borne the length of the ultimate segment, and decurrent along the stalk and often along the axis below, the margin commonly undulate, erose, and conspicuously fimbriate.

Many specimens of this variety not only have their ultimate segments very slender (8-10 times as long as broad) but have all pinnules drooping in pendulous fashion from each side of the pinna. Whether this condition results from maturity or habitat, or a combination of both, has not been satisfactorily determined.

Some authors have treated this as a synonym of the Mexican *C. hirsuta* Link, but perhaps both would be more properly considered varieties of *C. marginata*, under which see further discussion.

Cheilanthes radiata (L.) R. Br. ex J. Sm. J. Bot. (London) 4: 159. 1841. *Adiantum radiatum* L. Sp. Pl. 1094. 1753. *Adiantopsis radiata* (L.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 145. 1852. *Hypolepis radiata* (L.) Hook. Sp. Fil. 2: 72. 1852.

In forests and wooded ravines, 30-1,000 m.; Alta Verapaz; Escuintla; Huehuetenango; Izabal; Petén; San Marcos; Sololá. Mexico to Panama; West Indies; Colombia and Venezuela to Argentina and Paraguay.

Plants terrestrial; rhizome erect or ascending, provided with rigid, linear bicolorous scales, these 1-4 mm. long, with a blackish, sclerotic median stripe and narrow, brown, entire margins; leaves 20-55 cm. long, petiolate; petiole 10-50 cm. long, commonly longer than the lamina, terete, somewhat lustrous, atropurpureous, glabrous; lamina often nearly circular, consisting of (3) 5-9 pinnae all radiating from the same point at apex of petiole; pinnae 1-pinnate, thin- to firm-herbaceous, essentially glabrous, linear-lanceolate or narrow-elliptic, tapering to apex and to base, costae atropurpureous to blackish, subterete, appearing sulcate adaxially due to the presence of 2 conspicuous, perpendicular, herbaceous wings which are borne on each side the length of the pinna; pinnules numerous, less than 15 mm. long, subsessile or very short-stalked, hardly articulate but often readily and irregularly deciduous, inequilateral at base, cuneate basiscopically, truncate and commonly auriculate acropically, margins plane or scarcely revolute; veins distinct to (commonly) obscure, all but the basal ones simple; sori discrete, 5-10 on either margin; indusium a strongly modified and reflexed marginal flap, thin, greenish or brownish to scarious, glabrous, entire.

Some authors have maintained this species, along with about a dozen others, in the genus *Adiantopsis*, based principally on the characters of deciduous ultimate segments, alate costae, and strongly modified, discrete indusial flaps. Perhaps these characters are no weaker or more inconsistent than those now used to separate *Cheilanthes* from *Pellaea* or *Notholaena*, but I prefer to adhere to a more conservative classification until a complete revision is undertaken.

COCHLIDIUM Kaulfuss

REFERENCES: C. Christensen, *Cochlidium*, in: Taxonomic Fern Studies I, Dansk. Bot. Ark. 6 (3): 17-25. 1929. L. E. Bishop, Revision of the genus *Cochlidium*, Amer. Fern J. 68: 76-94. 1978.

Small, epiphytic plants; rhizome erect, provided with narrow, brown scales, these entire, not or scarcely clathrate; leaves monomorphic, fasciculate, not articulate, sessile or subsessile, coriaceous or subcoriaceous, simple and linear (in ours) or sometimes forked, 2-20 cm. long, 0.1-0.5 cm. broad, completely glabrous (as in ours) or with a few, scattered, very minute, 2- to 8-celled, catenate trichomes, margins entire (as in ours) or sinuate, the costa percurrent, indistinct or obscure, immersed in the tissue or often strongly raised adaxially; veins obscure, simple or forked, free, or sometimes anas-

tomosing, hydathodes commonly present (though often vestigial); sporangia stalked, borne on the veins very near the costa, forming one long coenosorus on either side, this continuous (in ours) or, rarely, interrupted, deeply immersed in the lamina in a central groove (as in ours) or superficial and occasionally spreading over the lamina surface; indusium lacking; paraphyses lacking or essentially so; spores trilete, tetrahedral, or globose-tetrahedral, commonly pale green (containing chlorophyll), mostly without perine.

Cochlidium is a small, neotropical genus very closely related to *Grammitis* (the suggestion has been made by a few to combine the two genera). It has been variously circumscribed by pteridologists, from a very strict sense—including only the two species with coenosori immersed in a deep central groove—to a very broad sense, with as many as 16 species. Bishop, in his recent revision (1978), adopted the latter option, whereby he includes not only the species with a central, immersed coenosorus, but also a number of species of *Grammitis* with superficial sori, both compound and discrete. However, I find that this course, instead of more clearly delineating the genus from *Grammitis*, tends to further obscure the lines of demarcation. The treatment unfortunately lacks descriptions of the genus or its species (save for the three novelties). Instead, *Cochlidium* is described simply in text as the “grammitid ferns with simple and entire . . . fertile laminae, concolorous scales, hydathodes, and 2-8-celled hairs which . . . are frequently catenate.” But there are many species of *Grammitis* with concolorous scales and hydathodes, and there are a few more with simple fertile laminae and others with minute, catenate trichomes.

I prefer to follow in large part Christensen's treatment of *Cochlidium* (1929), in which the species have: sporangia joined in a coenosorus, either deeply immersed in the lamina along a central groove (as in the Guatemalan species) or superficial and occasionally spread over the lamina surface; leaves essentially glabrous (lacking dark, spreading, unicellular trichomes, but occasionally with a few minute, scattered, pluricellular ones); lamina entire (in ours) to sinuate. Thus circumscribed, *Cochlidium* would include only 7-9 species, confined to the neotropics, the following two of which occur in Guatemala.

- a. Hydathodes distinct, visible with slight magnification; plants not occurring over 350 m. *C. linearifolium*.
- a. Hydathodes not evident, or scarcely so, and then only with high magnification; plants occurring at 800-2,100 m. *C. rostratum*.

***Cochlidium linearifolium* (Desv.) Maxon ex C. Chr.** Dansk Bot. Ark. 6 (3): 23. 1929. *Monogramma linearifolia* Desv. Ges. Naturf. Freunde Berlin Mag. Neusten Entdeck. 5: 302. 1811. *Grammitis linearifolia* (Desv.) Steudel, Nomencl. Bot. 2: 187. 1824.

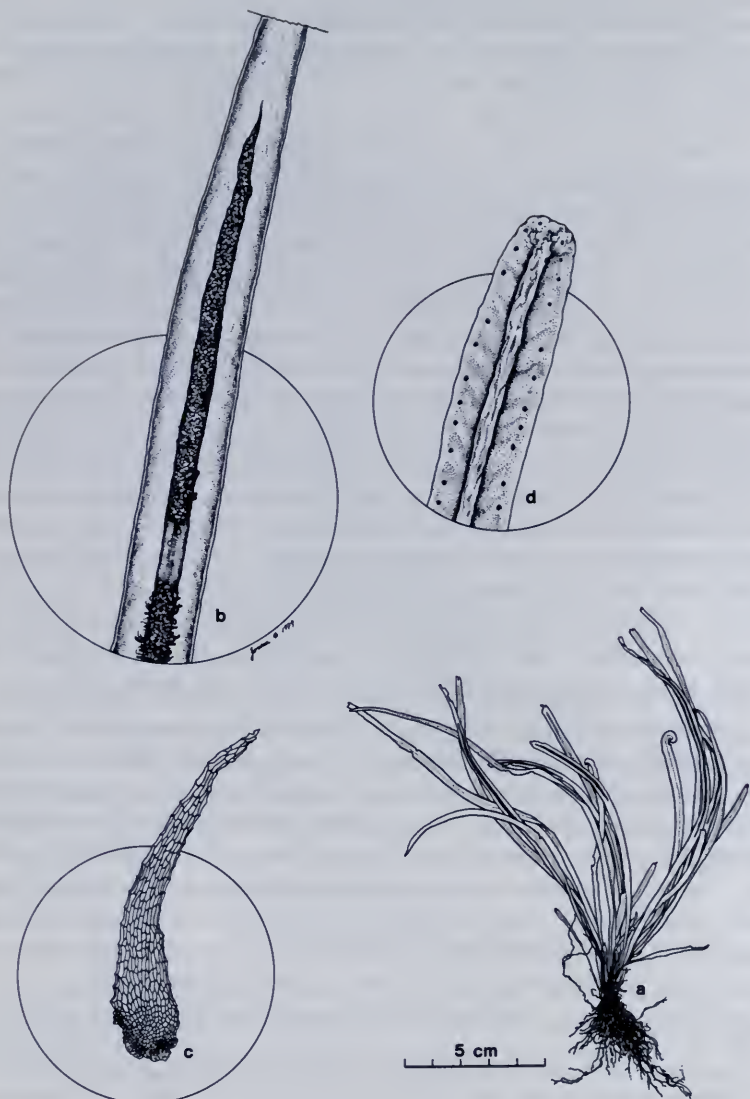


FIG. 18. *Cochlidium*. a-c, *C. rostratum*: a, habit, $\times \frac{1}{2}$; b, portion of lamina near apex, abaxial side, with sporangia removed to show central groove, $\times 6$; c, rhizome scale, $\times 25$; d, *C. linearifolium*, leaf apex, adaxial surface, $\times 6$.

In forests, on trunks of trees, sea level to 350 m.; Alta Verapaz; Izabal. British Honduras; Nicaragua to Colombia; French Guiana; Brazil.

Plants epiphytic; rhizome rather stout, erect, provided with orange or bright-brown, lanceolate scales, these 2-4 mm. long, not clathrate; leaves glabrous, 2-14 cm. long, 0.1-0.3 cm. broad, straight or strongly curved, sessile or very short-petiolate, linear, entire, flat, or often conduplicate in the fertile portion; veins obscure, simple (rarely 1-forked), free, terminating in small but commonly distinct hydathodes along the margin adaxially (these visible with only slight magnification); coenosori commonly confined to the distal half of the lamina, deeply sunken in a single, central groove along the midrib.

Cochlidium rostratum (Hook.) Maxon ex C. Chr. Dansk Bot. Ark. 6 (3): 23. 1929. *Monogramma rostrata* Hook. Sp. Fil. 5: 122. 1864. *C. rostratum* var. *areolatum* C. Chr. Dansk. Bot. Ark. 6 (3) 25. 1929.

In forests, on tree trunks or stumps, 800-2,100 m.; Alta Verapaz; Baja Verapaz; Chiquimula. Southern Mexico (Chiapas, Oaxaca); Honduras; El Salvador; Nicaragua to Colombia and Venezuela; Guadeloupe; Greater Antilles.

Plants epiphytic; rhizome rather stout and erect to elongated and ascending, provided with orange or bright-brown, lanceolate scales, these 2-3 mm. long, not clathrate; leaves glabrous, 4-20 cm. long, 0.1-0.3 cm. broad, straight or curved in a half-circle, sessile or very short-petiolate, linear, entire, flat, or often conduplicate in the fertile portion; veins obscure, simple (rarely 1-forked), free, or rarely casually anastomosing to form costal areoles, hydathodes not evident on the adaxial surface, or if so then visible only under very high magnification; coenosori commonly confined to the distal half of the lamina, deeply sunken in a single, central groove along the midrib.

This is scarcely distinct from *C. linearifolium* and should probably be considered merely a variety of it. The feature of distinct *vs.* obscure hydathodes is usually consistent with elevation of habitat, as noted in the key, but there are enough exceptions to this (as well as intermediate conditions) to render these weak characters even less reliable. Bishop (1978) uses the somewhat larger size of spores and sporangia of *C. rostratum* as an additional character, while admitting that this too has its exceptions.

CTENITIS Christensen

REFERENCES: Carl Christensen, Subgenus III, *Ctenitis* (pp. 82-112) in: A monograph of the genus *Dryopteris*, Part I . . . Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 55-282. 1913; and, Subgenus IX, *Ctenitis* (pp. 31-93) in: A monograph of the genus *Dryopteris*, Part II . . . *op. cit.* VIII. 6: 1-132. 1920. R. G. Stolze, New taxa and combinations of *Ctenitis* from Guatemala, Amer. Fern J. 67: 40-44. 1977.

Plants commonly terrestrial, rarely epipetric or epiphytic, a few larger species subarborescent; rhizome stout, erect or obliquely ascending (occasionally creeping), amply provided with entire, denticulate or (rarely) ciliate scales; leaves monomorphic, long-petiolate, commonly crowded or fasciculate; petiole not articulate, scaly (especially toward the base) like the rhizome, variously provided with unbranched, pluricellular, septate, usually short and reddish brown trichomes (these described by various authors as "*Ctenitis*-hairs"), abaxially rounded to obtusely angular, adaxially sulcate, often ridged within the groove; lamina pinnate-pinnatifid to 3-pinnate-pinnatifid, eglandular or variously beset with sessile or capitate glands, typically (especially on the axes) provided with short, septate trichomes, thin- or firm-herbaceous to subcoriaceous, ovate to broadly deltoid, or pentagonal due to the basiscopically produced basal pinnae, gradually tapering to a pinnatifid apex, lacking (except in a few species) a proliferous bud on the rachis; rachis not sulcate, or if so, the furrow not open to admit the furrow of the axis of the next order above, raised ridges (if any) of the adaxial side not continuous onto ridges or thickened leaf margins of axes of the next order above; pinnae usually many, spreading to ascending, frequently asymmetrical, with pinnules (especially basal ones) on one side of the costa much larger than those of the other side, costae not decurrent; pinnules typically catadromous, except rarely anadromous on basal pinnae; ultimate segments entire to crenate or serrate, not spinulose; venation essentially catadromous (rarely anadromous in basal segments of basal pinnae), veins free, simple or branched; sori abaxial on the veins or their branches; indusium relatively small and thin (rarely large and thick), circular-reniform, attached at the sinus, persistent, fugacious or lacking; paraphyses lacking; sporangium long-stalked, glabrous; spores monolete, with perine, commonly echinate.

For further elaboration on comparative diagnostic features, see discussion of *Lastreopsis*. *Ctenitis* is a pantropical genus of about 150 species, with much greater representation in the New World. Plants are of moderate to very great size, and a few species are subarborescent, with caudices rather stout and up to 0.5 m. long.

Christensen (1920) treated the genus in natural groups of species, which were based primarily on types of indument, and he provided a key to these groups. The following key to the species in Guatemala is not as "natural," but it should be more effective in separating the plants in our area.

- a. Lamina (above the basal pair of pinnae) pinnate-pinnatifid to nearly 2-pinnate or, rarely, fully 2-pinnate as to the bases of larger pinnae.
 - b. Basal pinnae greatly enlarged, commonly pinnate-pinnatifid and strongly produced basiscopically; indusia inconspicuous, fugacious; scales of the axes abundant, blackish, filamentous from a dilated base. *C. hemsleyana*.
 - b. Basal pinnae not or scarcely enlarged; indusia relatively large, subpersistent (except minute and fugacious in *C. nigrovenia* and *C. submarginalis*); scales various.
 - c. Segment margins sparsely to amply ciliate with minute, articulate trichomes (especially near the tips).
 - d. Scales of petiole and rachis lax, orange or light brown, with base flat or slightly revolute; sori medial or supramedial; ultimate segments subtire, most of them rounded or subacute at apex. *C. submarginalis*.
 - d. Scales of petiole and rachis rigid, reddish brown, atropurpureous, or blackish,

- the base bullate; sori (most of them) inframedial; ultimate segments serrate, most of them acute, apiculate. *C. strigilosa*.
- c. Segment margins eciliate.
- e. Most veins terminating short of margin; costal scales broad, bullate, with attenuate tips; indusium relatively large, subpersistent.
- f. Ultimate segments 4-6 (8) pairs; basal pair of pinnae as large as or larger than the rest; most pinnae asymmetrical near the base. ... *C. lanceolata*.
- f. Ultimate segments (8) 10-20 pairs in larger pinnae; basal pair of pinnae often smaller than those of the proximal half of the lamina; most pinnae essentially symmetrical throughout. *C. salvinii*.
- e. Most veins reaching the margin; costal scales linear to filiform (rarely with an expanded, subbullate base); indusium minute, fugacious (often apparently lacking on mature specimens). *C. nigrovenia*.
- a. Lamina 2-pinnate-pinnatifid to 4-pinnate or more.
- g. Scales of rachis and costa regularly and conspicuously spinulose-dentate or denticulate, narrow, most cells greatly elongated.
- h. Lamina commonly 2-pinnate-pinnatifid above the enlarged basal pinnae. *C. subincisa*.
- h. Lamina commonly 3-pinnate-pinnatifid above basal pinnae.
- i. Petiole amply to densely pilose; ultimate segments with margins, midribs and veins amply to densely hirsute or pilose. .. *C. pulverulenta* var. *pulverulenta*.
- i. Petiole glabrous to sparsely pilose; ultimate segments glabrous or with a few, rigid trichomes adaxially. *C. pulverulenta* var. *heydei*.
- g. Scales of rachis and costa entire, or if somewhat ciliate or denticulate, most cells isodiametric or slightly longer than broad.
- j. Ultimate segments densely long-pilose; scales of petiole base broad, ovate to lanceolate, most cells isodiametric or 2-3 times as long as broad. *C. pansamalensis*.
- j. Ultimate segments subglabrous, or the trichomes minute and scattered, sometimes marginal; scales of petiole base linear or filiform (flat and broad in *C. grisebachii*), most cells several to many times as long as broad.
- k. Rachis scales filiform, commonly spreading and tortuous, most of them 2-3 cells broad above the base; most cells several to many times as long as broad.
- l. Bullate scales abundant on costules and midrib abaxially; rachis scales abundant, reddish brown or blackish; indusium subpersistent, large, light brown with dark center. *C. melanosticta*.
- l. Bullate scales lacking, or rare and minute; rachis scales scattered, orange to light brown; indusium fugacious, minute, reddish brown. .. *C. interjecta*.
- k. Rachis scales ovate to linear-lanceolate, appressed or spreading, most of them 5 to many cells broad above the gradually expanded base; most cells 1-3 times as long as broad.
- m. Scales of rachis and bases of costae few, scattered, rigid, thick, not usually acuminate or attenuate to a filiform tip, the cells greatly elongated and essentially conform (*i.e.*, similar in shape, size, and color); scales of pinna axils few or lacking; indusium often rather large, dull brown, subpersistent to very late-deciduous. *C. grisebachii*.
- m. Scales of rachis and bases of costae ample to abundant, thin, lax, ovate and acuminate, or lanceolate and attenuate to a filiform tip, the cells nonconform (mostly isodiametric, but often elongated toward scale apex); scales of pinna

axils abundant; indusium (at least in Guatemalan species) lacking, or minute, reddish, early deciduous.

- n. Segment margins eciliate; rhizome scales orange; alt. 60-1,150 m.
C. excelsa.
- n. Segment margins sparsely to amply ciliate with minute, articulate trichomes; rhizome scales brown; alt. 1,300-2,700 m.
 - o. Scales of pinna axils and costae subentire, mostly lanceolate, vaulted and spreading, often blackish. *C. equestris* var. *equestris*.
 - o. Scales of pinna axils and costae erose and denticulate or short-ciliate, broad-ovate, flattened and appressed, mostly orange.
C. equestris var. *erosa*.

***Ctenitis equestris* (Kunze) Ching, Sunyatsenia 5: 250. 1940.**

Plants terrestrial; rhizome erect, stout, this and the petiole base abundantly provided with dull, light- to dark-brown, subentire, linear, often attenuate scales with elongated cells; leaves fasciculate, to 1.5 m. long, 0.5 m. broad; petiole to 0.8 m. long, light brown or stramineous, dark brown near the base, scales scattered or abundant, orange to reddish brown, or blackish, ovate and acute to lanceolate and attenuate, subentire (or the margins erose and irregularly ciliate in var. *erosa*); lamina commonly 3-pinnate-pinnatifid, or sometimes 4-pinnate-pinnatifid as to enlarged basal pinnae, firm-membranaceous to chartaceous, deltoid or deltoid-ovate, tissue usually glandular, sometimes densely so; rachis sulcate adaxially, light brown or stramineous, scaly as on the petiole, adaxially provided with reddish brown "*Ctenitis*-hairs" (at least in the channels); pinnae spreading to ascending, lower ones petiolulate, basal ones basiscopically enlarged and more highly dissected; pinnules subsessile or the larger ones short-stalked, commonly pinnate-pinnatisect or, in larger ones of basal pinnae more highly dissected, the costules adaxially reddish-pubescent, sparsely to densely provided abaxially with ovate to lanceolate, acuminate to attenuate scales, these either orange with margins erose and irregularly short-ciliate, or reddish brown to blackish and subentire, the cells mostly isodiametric, or somewhat elongated toward scale apex; ultimate segments oblong to subfalcate, obtuse to acute, subentire to serrate or lobed, margins and veins (and rarely the tissue between) ciliate with very minute, articulate trichomes, the midribs abaxially scaly as on the costules; veins evident, simple or forked, terminating at the margin; sori medial to inframedial, borne on the vein or its acroscopic branch; indusia (at least in Guatemala) lacking, or minute, reddish brown, very early fugacious.

This was included by Christensen (1920) in his "*Dryopteris ampla* group," a species complex as confused today as it was half a century ago. The entire group is badly in need of revision, and it is possible that most of the species which were circumscribed within it—*D. ampla*, *D. equestris*, *D. excelsa*, and *D. nemophila*—are conspecific. Morton (Amer. Fern J. 59: 66. 1969) cleared up much of the nomenclatural mess involving *Dryopteris ampla*, so that Christensen's concept of *D. ampla* is now properly known as *Ctenitis sloanei* (Poepp.) Morton, and true *D. ampla* is the South American *C. ampla* (H. & B. ex Willd.) Ching (Christensen's *D. nemophila*). However, it is evident that Christensen's species concepts in this group were not altogether clear.

For example, his key and descriptions point to "*D. ampla*" as having ciliate segment margins, but a number of specimens he cites are obviously eciliate. The latter should have been included under *C. excelsa*, an eciliate species which Christensen described as being confined to a few Lesser Antillean islands. He also proposed for his *D. equestris* the two new varieties *mentiensi* and *heterolepis*. The former supposedly differed from the typical in the shape and remoteness of ultimate segments, characters which quite naturally vary with the relative size of the leaf. The latter is probably not *C. equestris* at all, but more likely *C. excelsa* (under which see further discussion).

For purposes of this Flora, *C. equestris* is being maintained as a distinct species, apparently differing from *C. sloanei* (Christensen's *D. ampla*) in its darker and less numerous scales. Scales, especially of the axils and the costules, tend to be rather rigid and blackish, with the cells very distinct, and are most commonly somewhat vaulted. Specimens generally recognized as *C. sloanei* have been reported from Costa Rica to northern South America and Trinidad and are scattered through the Greater Antilles. Costular and axillary scales tend to be lighter in color, usually orange, flat and flaccid, and the petiole base is commonly covered with a dense, wooly mass of orange, hairlike scales. These in *C. equestris* are often darker, and only rarely form a dense tuft. However, enough specimens have been observed in each of the species to indicate a certain amount of variability in the shape, color, and density of scales, so that the efficacy of even this character remains suspect.

Ctenitis equestris var. **equestris**. *Aspidium equestre* Kunze, Linnaea 18: 347. 1844. *Lastrea ciliata* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 273 (seors. 121). 1849. *Aspidium scabriusculum* Daven. Bot. Gaz. 21: 255. 1896. *Dryopteris davenportii* C. Chr. Index Fil. 260. 1905. *D. equestris* (Kunze) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII. 6: 54. 1920. *D. equestris* var. *mentiensi* C. Chr. tom. cit. 56 (type from Cobán, Alta Verapaz. *Tuerckheim II-2118*).

In deep forests, on slopes, or in ravines, 1,300-2,500 m.; Alta Verapaz; Chimaltenango; Escuintla; Guatemala; Jalapa; Quezaltenango; Sacatepéquez; Zacapa. Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama.

Scales of rachis and upper petiole ample to scattered, commonly spreading and reddish brown or blackish, ovate-lanceolate to linear-lanceolate, attenuate, margin subentire; scales of pinna axils similar to those of rachis, mostly blackish, the cells somewhat

elongated (at base of scale sometimes isodiametric); scales of costule reddish brown to blackish, rigid and spreading, commonly vaulted; indusium (at least in Guatemala) light- or red-brown, glandular, very early fugacious.

I have examined several specimens from Chiapas, loaned to me from the Dudley Herbarium, in which the indusia are relatively large and persistent. Christensen (1920) also stated that he had seen some Mexican specimens with subpersistent indusia. But in all Guatemalan specimens seen indusia are minute and fugacious. Nevertheless, I agree with Christensen's observation that "indusiate and exindusiate forms are perfectly similar, and I have not succeeded in finding any other constant character by which they were to be distinguished from each other."

Some specimens from Nicaragua, and most from Costa Rica and Panama, are much more densely glandular on the abaxial surface of the lamina. These probably correspond to the plants described by Christensen as *Dryopteris ampla* var. *subdryopteris* (Christ) C. Chr. (*tom. cit.* 53), which he claimed also differed from *C. equestris* by softer texture and more lanceolate axillary scales. Most certainly these are *C. equestris*, not "*Dryopteris ampla*" (= *C. sloanei*), but whether they deserve further distinction as yet another form or variety is a moot point. Plants of var. *equestris* in Guatemala are slightly or not at all glandular.

***Ctenitis equestris* var. *erosa* Stolze, Amer. Fern J. 67: 41. 1977.**

Along banks of streams and in ravines, in deep forests, 2,400-2,700 m.; Chimaltenango; Quezaltenango; San Marcos (type from slopes of Cerro Tumbador, *L. O. Williams et al.* 23084). Southern Mexico.

Scales of upper petiole, rachis and pinna axils abundant, often imbricate and fully concealing the axis, orange (sometimes reddish brown in center), commonly broad-ovate, acute to acuminate, margins erose and irregularly denticulate or short-ciliate, mostly firmly appressed, the cells mostly isodiametric (sometimes elongated toward scale apex); scales of the costule orange, flaccid, flattened; indusium lacking.

It is unfortunate that another variety should be described for a species which is already confused and greatly misunderstood, and eventually very apt to be reduced to varietal status itself. However, in var. *erosa* the scales of the rachis and costae are the most distinctive in the entire species complex of *C. equestris-excelsa-sloanei*. Laminar scales throughout the complex are commonly slender (at most narrow-ovate), the margins essentially entire, and most of them spread somewhat from the axes. The laminar scales in var. *erosa* are often nearly as broad as long, the margins are erose and either irregularly denticulate or short-ciliate, and most of them are tightly appressed to the axes.

Ctenitis excelsa (Desv.) Proctor, *Rhodora* 63: 34. 1961. *Polypodium excelsum* Desv. Mém. Soc. Linn. Paris 6: 243. 1827. *Dryopteris excelsa* (Desv.) C. Chr. Index Fil. 264. 1905.

In deep, wet forests and thickets, often along streams, rivers, and marshes, 60-1,150 m.; Alta Verapaz; Chimaltenango; Escuintla; Izabal; Petén; Retalhuleu; Santa Rosa; Sololá. Southern Mexico; British Honduras; Honduras; El Salvador; Costa Rica; Panama; Guadeloupe; Dominica; Martinique.

Plants terrestrial; rhizome erect, stout, this and petiole base provided with a dense matting of orange, linear or filiform, attenuate scales with elongated cells; leaves fasciculate, to 1.5 m. long, 0.6 m. broad; petiole to 0.7 m. long, light brown to stramineous, above the base amply provided with dark-brown to blackish (or rarely orange) scales, these subentire, often appressed, linear and attenuate to narrow-ovate and acuminate; lamina 3-pinnate-pinnatifid, or sometimes 4-pinnate-pinnatifid as to enlarged basal pinnae, chartaceous to subcoriaceous, deltoid-ovate, tissue usually glandular, sometimes inconspicuously so; rachis sulcate adaxially, light brown or stramineous, scaly as on the petiole (except more often linear and attenuate at pinna axils), adaxially provided with orange or reddish brown "Ctenitis-hairs" (though proximally often only in the channels); pinnae spreading to ascending, short-stalked (or the proximal ones to 10 cm.), basal ones basiscopically enlarged and often more highly dissected, the costae with scattered, dark, attenuate, often vaulted scales; pinnules (at least the proximal ones) short-stalked, commonly pinnate-pinnatisect, or in larger ones of basal pinnae more highly dissected, the costules sparsely to amply provided on abaxial side with orange to dark-brown, lanceolate, attenuate scales; ultimate segments oblong to subfalcate, obtuse to acute, subentire to serrate or lobed, midribs abaxially with a few minute scales and on both sides with a few minute trichomes, margins eciliate; veins evident, simple or forked, terminating at the margin; sori medial to inframedial, borne on the vein or its ascropic branch; indusia lacking.

Christensen suggested (1920) that this may be a variety of "*Dryopteris ampla*" (= *C. sloanei*), and he is probably correct. He pointed out that plants of *D. ampla* are confined to Martinique, Dominica, and Guadeloupe and "are remarkably constant as to certain characters" (viz., the margins eciliate, the scales on costules and midribs ovate, blackish, and vaulted). However, I have found some plants from Central America to be perfect matches for the Antillean ferns, and yet there are others from Guatemala and southern Mexico which, at least in the shape and color of scales, more closely resemble *C. sloanei*. So the scale characters are *not* so constant as Christensen thought, and *C. excelsa* may turn out to be but another element in the extremely variable *C. ampla-sloanei* complex.

With *C. excelsa* probably should be included Christensen's *Dryopteris equestris* var. *heterolepis*, of Costa Rica and Panama. I have examined the type collection of the latter and find it rather closely matches most collections of *C. excelsa*, especially in that the ultimate

segments are eciliate. Although Christensen used this character in delineating several other species of *Ctenitis*, he apparently ignored it in his description of var. *heterolepis*, which makes no reference to segment margins. However, his species description of *D. equestris* does refer to "Upper surface with *Ctenitis*-hairs along . . . edges." So, whatever status is assigned, it certainly seems more closely affiliated with *C. excelsa* than with typical *C. equestris*.

Ctenitis grisebachii (Bak.) Ching, Sunyatsenia 5: 250. 1940. *Nephrodium grisebachii* Bak. in Hook. & Bak. Syn. Fil. 285. 1867. *Dryopteris grisebachii* (Bak.) O. Ktze. Rev. Gen. Pl. 2: 812. 1891. *C. molinae* Stolze, Amer. Fern J. 67: 40. 1977.

In wet forests, on slopes, or on banks of streams or ravines, 1,200-1,800 m.; Chimaltenango; Quezaltenango. Southern Mexico (Chiapas); Honduras; Nicaragua; Cuba; Jamaica; Hispaniola.

Plants terrestrial; rhizome erect or obliquely ascending, provided with deep-orange, linear-lanceolate scales, these 1.5-2.5 cm. long and 0.2-0.4 cm. broad; leaves fasciculate, to 1.5 m. long and 0.6 m. broad; petiole to 0.7 m. long, brown or yellowish, muricate with reddish, raised persistent scale bases and provided with scattered, rigid, thick, lustrous, deep-orange or castaneous scales, these to 8 mm. long, commonly spreading, linear or linear-lanceolate, with margins entire and most cells greatly elongated and essentially conform (*i.e.*, similar in orientation, shape, size, and color); lamina 2-pinnate-pinnatifid to nearly 3-pinnate, or rarely 3-pinnate-pinnatifid as to bases of the lowest pinnae, firm-membranaceous, subdeltoid-ovate, tissue commonly minutely glandular on both sides; rachis stramineous to light or dark brown, lustrous, muricate, and scaly as on the petiole, terete abaxially, trisulcate adaxially, the grooves amply provided with reddish "*Ctenitis*-hairs"; pinnae slightly ascending, often subopposite, lower ones short-stalked, scales of the axils few or lacking, scales of the costae abaxially like those of the petiole and rachis, but much smaller and with cells not so elongated, costae and costules adaxially provided with orange or reddish "*Ctenitis*-hairs"; ultimate segments oblong to subfalcate, entire to crenate, obtuse or subacute, glabrous except for a few, minute, articulated trichomes on the midrib adaxially, the margins eciliate or very sparsely and minutely ciliate; veins evident or somewhat obscure, simple, or 1-forked in deeply crenate segments, terminating at or very near the margin; sori mostly inframedial on the veins; indusium dull brown or yellowish, often rather large, subpersistent or very late fugacious, glandular-ciliate.

Although Christensen (1920) included this in his group of *Dryopteris hirta*, I feel it might be as easily placed in his *Dryopteris ampla* group, for in most characters it resembles species such as *Ctenitis equestris* and *C. excelsa*. However, the scales of the axes are quite distinctive. Those of the "*ampla*-group" are typically very abundant, and in places such as the rachis and pinna axils they may be so dense in some species as to nearly obscure the surface of the axis. They are usually thin-textured, relatively broad, acuminate or long-attenuate, and the cells



FIG. 19. *Ctenitis*. a, *C. excelsa*, habit, rhizome, and pinna, $\times \frac{1}{2}$; b, *C. lanceolata*, habit, $\times \frac{1}{2}$; c, *C. interjecta*, portion of rachis and pinna base, adaxial side, $\times 10$; d-e, *C. melanosticta*: d, portion of rachis with trichomes, $\times 25$; e, portion of pinnule, abaxial side, with sori and bullate scales, $\times 15$; f, *C. grisebachii*, rachis scales, $\times 18$; g, *C. strigilosa*, rachis scales, $\times 18$; h, *C. subincisa*, rachis scales, $\times 18$.

are mostly isodiametric or nearly so. Scales of *C. grisebachii* are scattered, those of the primary axis very rigid and thickened, linear, and not usually strongly tapered at apex. The cells are very thick as seen in cross-section, often thicker than broad, and most of them are very narrow and greatly elongated. The scale base usually is not expanded, but is quite firm and usually persistent, even when the rest of the scale has been broken off. Thus the rachis and petiole are often conspicuously reddish-muricate throughout.

This was recently published (1977) as a new species, *C. molinae*, at which time I described the specimens as being closely related to *C. grisebachii*. It appeared to me that the latter differed in its smaller, more fugacious indusia, thinner leaf texture, more highly dissected lamina, and the axes dark brown rather than stramineous. This comparison was based on Christensen's rather detailed description in part 2 of his monograph (1920) and on the few Antillean specimens in the Field Museum herbarium. Since the publication of *C. molinae* I have had the opportunity to study more collections at U.S. National Herbarium, and Alan Smith kindly sent some Chiapas specimens from the University of California herbarium which he believed to be *C. grisebachii*. Apparently size of indusium, color of axes and texture, and dissection of lamina are highly variable and inconsistent when compared throughout a large number of collections, so much so that there is evidently no basis for distinguishing groups of specimens even at infraspecific level.

Ctenitis hemsleyana (Bak. ex Hemsl.) Copel. Gen. Fil. 124. 1947.
Polypodium hemsleyanum Bak. ex Hemsl. in Biol. Centr. Amer. 3: 660, t. 108. 1885 (type from Chilasco, *Godman & Salvin s.n.*). *Dryopteris hemsleyana* (Bak. ex Hemsl.) C. Chr. Index Fil. 270. 1905.

In forests and thickets, often on banks of ravines, 1,200-2,600 m.; Alta Verapaz, Baja Verapaz; Jalapa; San Marcos; Santa Rosa; Zacapa. Southern Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama.

Plants terrestrial; rhizome erect or obliquely ascending, provided with reddish brown or blackish, lustrous, opaque, ovate to linear-lanceolate scales; leaves crowded to fasciculate, mature ones 0.3-1.3 m. long and 0.2-0.35 m. broad; petiole 20-75 cm. long, about as long as the lamina, yellowish to dark brown, densely covered with spreading, hairlike, reddish brown or blackish scales, these to 8 mm. long, subentire, lustrous, with revolute margins, filiform tips and enlarged, subbullate bases; lamina essentially pinnate-pinnatifid to nearly 2-pinnate, but 2-pinnate-pinnatifid as to the enlarged basal pair of pinnae, firm-membranaceous to chartaceous, deltoid or sometimes subpentagonal, acute at the pinnatifid apex, eglandular or both surfaces lightly provided with minute, ap-

pressed, rodlike, reddish glands; rachis yellowish to dark brown, densely scaly as on the petiole, adaxially densely covered with short, stout, septate trichomes; pinnae spreading or slightly ascending, rarely crowded, sessile, or the lower ones short-stalked, all but the basal pair pinnatisect and symmetrical, the latter commonly pinnate-pinnatisect and greatly enlarged, especially so basiscopically, therefore strongly asymmetrical; costa densely septate-pubescent adaxially, the abaxial side amply provided with scales like those of the main axis, though often shorter, less attenuate, and more obviously bullate at base; ultimate segments subentire to deeply crenate-serrate, subfalcate, acute; veins 6-9 pairs, simple, terminating at or very near the margin; sori 1 to a vein, inframedial between midrib and segment margin, commonly confined to the proximal two-thirds of each segment; indusium fugacious, relatively small and inconspicuous, light or reddish brown, essentially eglandular, margins subentire, erose or with a few, short cilia.

Due to the unique character of the lamina, this species is one of the easiest of the genus to recognize. Most of the larger pinnae are symmetrical, deeply pinnatisect, and of similar size and shape; but the basal pair are greatly enlarged, fully pinnate-pinnatisect, and strongly asymmetrical, the basal basiscopic pinnules often 2-3 times larger than the opposing acroscopic ones. On typical plants, each of the basal pinnae may be half as long and broad as the rest of the lamina, so that the leaf appears nearly tripartite. *Ctenitis hemsleyana* is most closely related to *C. strigilosa*, and in specimens lacking basal pinnae, the two are extremely difficult to separate. However, ultimate segments are glabrous adaxially in *C. hemsleyana*, or provided with a few typical "*Ctenitis*-hairs" along the midribs. In *C. strigilosa* the segments are sparsely to amply provided, on the adaxial side, with minute septate trichomes which are usually gland-tipped. These are most evident along the margin.

Ctenitis interjecta (C. Chr.) Ching, Sunyatsenia 5: 250. 1940.
Dryopteris interjecta C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII. 6: 43. 1920.

In forests, often along rivers or streams, 350-420 m.; Alta Verapaz (type from Cubilguitz, *Tuerckheim s.n.* ed. Donn.-Sm. 8049); Izabal. Southern Mexico; British Honduras; Honduras.

Plants terrestrial; rhizome not seen; leaves to 1.25 m. long, 0.5 m. broad; petiole to 0.6 m. long, light or yellowish brown, the base often darker brown and provided with a dense tuft of orange, linear to filiform, entire, long-attenuate scales, these with cells several to many times longer than broad; lamina commonly 2-pinnate-pinnatisect, or rarely nearly 3-pinnate as to bases of largest pinnae, thin- to firm-membranaceous, ovate or deltoid, tissue with sessile glands minute and inconspicuous or lacking; rachis (and most of petiole) sparsely provided with tortuous, filiform, orange or light-brown trichomes; pinnae subopposite, ascending, short-stalked, nearly as long or slightly longer than the rest, costae and costules sparsely provided with orange or light-brown, filiform scales abaxially, abundant reddish "*Ctenitis*-hairs" adaxially; pinnules oblong-

lanceolate, sessile, basiscopically adnate or decurrent, acute to acuminate; ultimate segments oblong to subfalcate, acute, entire to sharply serrate, subglabrous, veins evident, simple or forked, terminating short of the margin; sori medial, borne on the vein or its acroscopic branch; indusia minute, reddish brown, ciliate, fugacious.

Ctenitis lanceolata (Bak.) A. R. Smith, Proc. Calif. Acad. Sci. 40: 229. 1975. *Nephrodium lanceolatum* Bak. Syn. Fil. ed. 2, 498. 1874 (type from Cobán, Alta Verapaz, *Salvin & Godman s.n.*). *Dryopteris lanceolata* (Bak.) O. Ktze. Rev. 2: 813. 1891. *Nephrodium tricholepis* Bak. in Hemsl. Biol. Centr. Amer. 3: 651. 1885 (type from Cobán, Alta Verapaz, *Salvin s.n.*). *Dryopteris tricholepis* (Bak.) C. Chr. Index Fil. 298. 1905. *D. lanceolata* var. *deltoideo-lanceolata* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 107. 1913 (type from Cobán, Alta Verapaz, *Tuerckheim II-1621*). *D. lanceolata* var. *tricholepis* (Bak.) C. Chr. loc. cit.

In forests, on or among rocks in shaded ravines, rarely at the bases of trees, 800-1,600 m.; Alta Verapaz; Huehuetenango.

Plants terrestrial or epipetric; rhizome erect, ascending or short-creeping, provided with dark-brown, slightly lustrous, lanceolate scales; leaves crowded to fasciculate, mature ones 15-50 cm. long, 3.5-8 cm. broad; petiole 6-18 cm. long, slightly shorter than the lamina, yellowish to dark brown, provided with short, septate trichomes adaxially, variously scaly, the basal scales much like those of the rhizome, the more distal ones becoming narrower and attenuate from a broad base; lamina deltoid- to oblong-lanceolate (basal pinnae about as large as or larger than the rest), typically pinnate-pinnatisect, or sometimes nearly 2-pinnate as to bases of larger pinnae, but often the basal pair of pinnae somewhat enlarged and more highly dissected, these frequently pinnate-pinnatifid, leaf tissue thin- to firm-membranaceous and essentially glabrous and eglandular; rachis yellowish or light brown, densely septate-pubescent adaxially, on the abaxial side abundantly scaly as on the petiole, the scales on the distal portion becoming shorter, with broader, bullate bases; pinnae 10 to many pairs, the distal and medial ones sessile and spreading or slightly ascending, the proximal ones often short-stalked and somewhat deflexed, incised nearly (or at the base quite) to the costa, often asymmetrical, with the acroscopic segments somewhat reduced, the costa pubescent adaxially, abundantly scaly abaxially, the scales dark brown to blackish, bullate, attenuate to a filiform apex; ultimate segments 4-6 (8) pairs, often subdistant, joined by a usually broad sinus, entire, eciliate, crenate-serrate, or lobed, strongly oblique, obtuse or subacute at apex, asymmetrical at base, broadly cuneate acroscopically, adnate or decurrent basiscopically; veins 2-6, simple, or rarely 1-forked in the lobes of enlarged basal pinnae, terminating short of the segment margin; sori 1 to a vein, attached inframedially between midrib and segment margin; indusium light or dark brown, persistent, margin subentire to erose or deeply crenate.

Christensen (1913) described vars. *tricholepis* and *deltoideo-lanceolata*, the latter for its slightly more dissected lamina, and the former in that it was "a smaller plant than the type." Neither is a valid reason for varietal distinction.

Ctenitis melanosticta (Kunze) Copel. Gen. Fil. 124. 1947. *Aspidium melanosticta* Kunze, Linnaea 13: 148. 1839. *Polystichum melanostictum* (Kunze) Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 276 (seors. 124). 1849. *Aspidium extensum* Fée, Mém. Fam. Foug. 5: 294. 1850-52. *nom. illeg.* *A. expansum* Fée, op. cit. 10: 42. 1865. *Dryopteris melanosticta* (Kunze) O. Ktze. Rev. Gen. Pl. 2: 813. 1891. *D. melanosticta* var. *bullata* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII. 6: 43. 1920.

In wet forests and thickets, often on banks of rivers or ravines, 50-1,000 m.; Alta Verapaz; Izabal; Petén. Mexico; British Honduras; Honduras; Costa Rica.

Plants terrestrial; rhizome stout, erect to ascending, the apex densely covered with a cluster of bright, brown, linear, entire, attenuate scales, these with cells several to many times longer than broad; leaves to 1.3 m. long, 0.6 m. broad; petiole to 0.6 m. long, light or yellowish brown, often darker below, this and the rachis abundantly provided with entire, filiform, orange to dark-brown scales as on the rhizome, these often spreading and tortuous, commonly 2-3 cells broad above a dilated, sometimes subbullate base; lamina commonly 2-pinnate-pinnatisect, or 3-pinnate-pinnatifid as to the largest pinnae, thin- to firm-membranaceous, ovate or subdeltoid, tissue often lightly or sparsely dotted with sessile, yellow or orange glands; rachis light brown to stramineous; pinnae ascending, sessile (or proximal ones short-stalked), basal ones somewhat or only slightly larger than the rest; costae and costules amply provided abaxially with bullate scales with attenuate, filiform tips, adaxially with abundant, reddish "Ctenitis-hairs"; pinnules oblong-lanceolate or deltoid-lanceolate, sessile, basiscopically adnate or decurrent, acute to acuminate; ultimate segments oblong to subfalcate, acute, entire to sharply serrate, subglabrous (rarely with scattered, minute, articulate trichomes along the margin, or a few bullate scales on the midrib abaxially); veins evident, simple or forked, terminating short of the margin; sori medial to inframedial, borne along the veins or their acroscopic branches; indusia reniform, persistent, thin, flat, commonly bicolorous, reddish brown, with light-brown, short-ciliate margin, or mostly light brown with a deep red or blackish center spot.

Many Guatemalan species of *Ctenitis* are exindusiate, or the indusia are minute and very early fugacious. However, the indusium in *C. melanostica* is large, persistent, and usually bicolorous. The dark center is highly variable, often filling more than half the area of the indusium, yet frequently it is merely a small dot which may be obscured by the constricted margins of mature indusia.

Ctenitis nigrovenia (Christ in Donn.-Sm.) Copel., Gen. Fil. 124. 1947. *Nephrodium nigrovenium* Christ, in Donn.-Sm. Bot. Gaz. 20: 545. 1895. *Dryopteris nigrovenia* (Christ) C. Chr. Index Fil. 279. 1905. *C. thelypteroides* A. R. Smith, Proc. Calif. Acad. Sci. 60: 215. 1975.

In forests, on banks of rivers and ravines, 200-1,800 m.; Petén;

Santa Rosa. Southern Mexico; Honduras; Nicaragua; Costa Rica; Panama; Colombia; Venezuela; Trinidad.

Plants terrestrial; rhizome short-repent to obliquely ascending or erect, provided with subentire, dark-brown, somewhat lustrous, ovate to lanceolate scales; leaves crowded, usually fasciculate, mature ones 35-70 cm. long, 10-20 cm. broad; petiole 20-35 cm. long, equal to or slightly shorter than the lamina, dark brown or yellowish brown, septate-pubescent adaxially, amply provided with dark-brown, spreading, linear, attenuate scales, these subentire, flat, or sometimes subbullate at the abruptly broadened base; lamina deltoid, subdeltoid to narrow-ovate, broadest at or near the base, pinnate-pinnatisect; leaf tissue firm-membranaceous, abaxially provided (often sparsely and minutely) with orange or yellow glands; rachis yellowish or light brown, septate-pubescent adaxially, the abaxial side provided with dark reddish brown or blackish, linear to filiform scales, these 1-3 mm. long with an expanded or subbullate base; pinnae numerous, spreading to slightly ascending, or the basal pair somewhat deflexed, sessile or a few very short-stalked, incised nearly to the costa, essentially symmetrical, the costae abaxially provided with reddish brown to blackish, filiform scales, some of these occasionally with an expanded, subbullate base; ultimate segments entire to crenate-serrate, spreading or slightly oblique, obtuse to subacute at apex, margins eciliate; veins commonly 5-8 pairs, simple, most of them reaching the margin; sori medial to inframedial or often in a V-shaped pattern on the segment (supramedial at base, but crowding the costa near the segment apex); indusium minute, dark, reddish brown, early fugacious (thus mature specimens often apparently exindusiate).

This species has a rather wide, albeit scattered, distribution in the neotropics, but nowhere has it been collected in abundance. There has been some confusion in identifying specimens of this and *Dryopteris* (*Ctenitis*) *tonduzii* of Costa Rica (see further discussion under "Excluded Species"), and the taxonomy needs further clarification.

Alan R. Smith has recently named a new species, *C. thelypteroides*, from Chiapas, Mexico, and cites one specimen from Petén (Lundell 18115). This is suggested as being very closely related to *C. nigrovenia*, but distinguished from it primarily by the crowded, reduced basal pinna segments and by the sori being localized at the segment tips. I have examined the types and paratypes, and these characteristics at first appear to be distinctive, especially in this narrow geographical area. However, I have had the opportunity to study various herbarium collections of *C. nigrovenia* and *D. tonduzii*, throughout the range of both, and find that often enough there appears to be a tendency in these species for the sori to localize near the tips of segments (or at least on their distal half). Furthermore, it is not at all uncommon to find the lower pairs of pinnae of both species with some reduced and crowded basal segments. Therefore, for the purposes of this treatment, I am maintaining *C. thelypteroides* in synonymy with *C. nigrovenia*.

Ctenitis pansamalensis (C. Chr.) Ching, *Sunyatsenia* 5: 250. 1940.
Dryopteris pansamalensis C. Chr. Kongel. *Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII.* 6: 72. 1920.

In dense, wet forests, 600-1,200 m. Alta Verapaz (type from Pansamalá, *Tuerckheim 1055*). Southern Mexico (Chiapas).

Plants terrestrial, acaulescent; leaves to over 1 m. long and 0.7 m. broad; petiole to 40 cm. long and 0.7 cm. in diameter, yellowish brown, sparsely provided with articulate trichomes, but rather amply provided (especially at base) with dark-brown, flat, broad, thin, mostly appressed scales, these sometimes attenuate, with margins entire or (very rarely) minutely and remotely denticulate, the cells isodiametric, or distal ones 2-3 times as long as broad; lamina commonly 2-pinnate-pinnatifid, or 3-pinnate-pinnatifid as to enlarged basal pinnae, membranaceous, subdeltoid, tissue eglandular or essentially so; rachis yellowish brown, this and the costae amply provided with broad, appressed scales and "*Ctenitis*-hairs," the latter much longer and more abundant on the adaxial side; pinnae subopposite, ascending, short-stalked, basal ones basiscopically enlarged and more highly dissected; pinnules oblong or oblong-lanceolate, sessile and obtuse to acute, or largest ones short-stalked and acuminate; tertiary segments oblong, broadly rounded to truncate at the apex, entire to crenate, or cut nearly to the midrib in larger pinnules of proximal pinnae, the margins, midribs, and veins (and rarely the tissue between the veins) abundantly pilose; veins terminating short of the margin, obscure, simple or 1-forked from a rather flexuous midrib; sori medial to supramedial, borne along the veins or their acroscopic branches, exindusiate.

Ctenitis pulverulenta (Poir. in Lam.) Copel. *Gen. Fil.* 124. 1947.

Plants terrestrial, often arborescent, with stems to over 1 m. tall; leaves to 3 m. long and 1.5 m. broad; petiole to 2 m. long and 3 cm. in diameter, yellowish to dark brown, castaneous at base, glabrous to sparsely or abundantly pilose, at base abundantly provided with scales, these lustrous, castaneous, twisted, linear, attenuate, remotely and spinulose-dentate, most of the cells many times longer than broad; lamina commonly 3-pinnate-pinnatifid, or nearly 4-pinnate-pinnatifid as to enlarged basal pinnae, firm-membranaceous to chartaceous, deltoid or deltoid-ovate, tissue eglandular or essentially so; rachis gray- to yellow-brown, this and costae and costules abaxially provided with dark-brown, linear, spinulose-dentate scales, adaxially provided with abundant "*Ctenitis*-hairs," and commonly also with longer, whitish, less articulate trichomes; pinnae spreading to ascending, lower ones distinctly petiolulate, basal ones basiscopically enlarged and more highly dissected; pinnules subsessile or the larger ones short-stalked, commonly pinnate-pinnatisect or, in larger ones of lower pinnae, more highly dissected; tertiary segments (larger ones) acute, deeply pinnatisect; ultimate segments obtuse, entire or slightly crenate, the margins, midribs, and veins (and rarely the tissue between the veins) amply to abundantly hirsute or pilose (or in var. *heydei* essentially glabrous); veins several-branched in each segment, the branch tips terminating short of the margin, not or scarcely enlarged; sori medial or inframedial, borne about midway along vein branches, exindusiate.

Both var. *pulverulenta* and var. *heydei* occur in Guatemala. For comparison with other species, see discussion under *C. subincisa*.

Ctenitis pulverulenta var. **pulverulenta**. *Polypodium pulverulentum* Poir. in Lam. Encycl. Meth. 5: 555. 1804. *P. karstenianum* Kl. Linnaea 20: 390. 1847. *Nephrodium villosum* Presl var. *karstenianum* Jenm. Bull. Bot. Dept. n.s. 3: 104. 1896. *Dryopteris karsteniana* (Kl.) Hieron. Hedwigia 46: 348. 1907. *D. pulverulenta* (Poir. in Lam.) C. Chr. in Urban Symb. Antill. 9: 305. 1925. *C. karsteniana* (Kl.) Vareschi, Fl. Venez. 1: 405. 1969.

Known thus far from one collection in Guatemala: in mountains, between Tactic and Tamahú, alt. 1,500-1,600 m., Alta Verapaz (Standley 91509). Jamaica; Hispaniola; Mexico?; Honduras; Costa Rica; Colombia; Venezuela; Ecuador; Peru.

Petiole amply to densely pilose; ultimate segments with margins, midribs, and veins (and rarely the tissue between the veins) amply to densely hirsute or pilose.

Ctenitis pulverulenta var. **heydei** (C. Chr.) Stolze, Amer. Fern J. 67: 43. 1977. *Dryopteris karsteniana* (Kl.) Hieron. var. *heydei* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII. 6: 77. 1920.

In forests and on wooded slopes and ravine banks, often along streams or rivers, 800-2,300 m.; San Marcos; Santa Rosa (type from Rio de los Esclavos, Heyde & Lux s.n. [ed. Donn.-Sm. 3249 *pro parte*]).

Petiole glabrous to sparsely pilose; ultimate segments glabrous or rarely some rigid trichomes scattered on veins and midribs adaxially.

Apparently var. *heydei* occurs only in Guatemala, although Christensen (1920) stated that the specimens collected in Ecuador are often subglabrous.

Some Heyde and Lux specimens bearing Donnell-Smith's distribution number 3249 represent a mixed collection. Four of these have been examined at U.S. National Herbarium, all originally determined as *Nephrodium amplum* and each stamped with a different herbarium number. Numbers 258590 and 830986 are isotypes of *Dryopteris karsteniana* (= *Ctenitis pulverulenta*) var. *heydei*, but numbers 258596 and 830988 are *Ctenitis excelsa*.

Ctenitis salvinii (Bak.) Stolze, Amer. Fern J. 67: 43. 1977. *Nephrodium salvinii* Bak. in Hook. & Bak. Syn. Fil. 274. 1867 (type from Guatemala, Salvin & Godman s.n.). *Aspidium lindenii* Kuhn, Linnaea 36: 116. 1869. *A. lindenii* Fourn. Mex. Pl. 1: 97. 1872. *nom. illeg.* *Nephrodium lindenii* (Kuhn) Bak. in Hook. & Bak. Syn. Fil. ed. 2: 493. 1874. *Dryopteris lindenii* (Kuhn) O. Ktze. Rev. Gen. Pl. 2: 813. 1891. *D. salvinii* (Bak.) O. Ktze. loc. cit. *C. lindenii* (Kuhn) A. R. Smith, Proc. Calif. Acad. Sci. 40: 229. 1975.

On rocks or rocky slopes and outcrops, 75-350 m.; Alta Verapaz; Huehuetenango; Izabal. Southern Mexico; British Honduras.

Plants terrestrial or epipetric; rhizome stout, erect to ascending, provided with entire, dark-brown, lustrous, lanceolate scales; leaves fasciculate, mature ones 28-70 cm. long, 6-14 cm. broad; petiole 10-30 cm. long, commonly $\frac{1}{2}$ - $\frac{3}{4}$ the length of the lamina, yellowish or light brown, septate-pubescent adaxially, amply provided with dark-brown, linear, attenuate scales, these subentire, flat, or slightly revolute toward the abruptly broadened base; lamina lanceolate, often narrowly so, broadest near the middle, pinnate-pinnatisect, or nearly 2-pinnate as to bases of largest pinnae, leaf tissue firm-membranaceous, eglandular and glabrous; rachis yellowish or light brown, septate-pubescent adaxially, the abaxial side provided with brownish, bullate scales, these attenuate with long, filiform tips; pinnae numerous, spreading, or slightly ascending, sessile to short-stalked, incised nearly to the costa, essentially symmetrical (acroscopic and basiscopic segments subequal), the costae abaxially provided with bullate scales; ultimate segments (8) 10-20 pairs on larger pinnae, crowded, entire, crenate-serrate or (rarely) lobed, slightly oblique, obtuse to subacute at apex, often adnate at the basiscopic base, margins eciliate; veins commonly 3-5 pairs, simple, or rarely 1-forked in enlarged, lobed, basal segments, terminating short of the segment margin; sori one to a vein, medial or supramedial; indusium brown, persistent, subentire to irregularly crenate, glandular, glabrous or, more commonly, with a few, minute, marginal cilia.

There is no good reason to maintain this and *C. lindenii* as separate species. The latter was said to be less robust and to have less deeply serrated segments. The two differ in no significant characteristics.

Ctenitis strigilosa (Dav.) Copel. Gen. Fil. 125. 1947. *Aspidium strigilosum* Dav. Bot. Gaz. 21: 257. 1896. *Dryopteris strigilosa* Dav. loc. cit. *D. strigilosa* var. *cookii* Maxon (pro. sp.) ex C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 105. 1913 (type from Alta Verapaz, Cook & Griggs 507).

In forest, often along streams, or on limestone cliffs or outcrops, 830-1,440 m.; Alta Verapaz. Mexico (Veracruz).

Plants terrestrial or epipetric; rhizome erect or obliquely ascending, provided with entire, dark-brown to blackish, lustrous, linear or lanceolate scales; leaves crowded to caespitose, mature ones 30-60 cm. long, 6-18 cm. broad; petiole 9-24 cm. long, slightly shorter than or $\frac{1}{2}$ the length of the lamina, yellowish or (commonly) dark brown, amply to densely provided with spreading, dark-brown or blackish, linear, often filiform, entire scales; lamina narrow-deltoid, pinnate-pinnatisect, or nearly 2-pinnate as to the bases of lower pinnae; leaf tissue firm-membranaceous, abaxially provided (often sparsely) with orange or yellow glands; rachis yellowish or dark brown, densely septate-pubescent (especially adaxially), the abaxial side provided with dark reddish brown or blackish, linear to filiform scales, these 2-5 mm. long with an expanded or subbullate base; pinnae numerous, spreading to ascending, or the basal pair somewhat deflexed, sessile, or the lower ones short-stalked, incised nearly (or basally, quite) to the costa, nearly symmetrical, or sometimes several proximal basiscopic segments shorter than the acroscopic ones, the costae provided with abundant short "*Ctenitis*-hairs" and a few scattered, longer ones, and also abaxially with reddish brown to blackish filiform scales, some of

these with an expanded, subbullate base; ultimate segments entire to crenate-serrate, mostly oblique, acute, margins sparsely to amply ciliate with minute, articulate trichomes (especially near the segment tip); veins commonly 7-11 pairs, simple to 1-forked, most of them reaching the margin; sori medial to (most commonly) inframedial; indusium conspicuous, orange to dark, reddish brown, persistent.

This is most closely related to, and might be confused with, *C. hemsleyana*, under which see further discussion.

Ctenitis subincisa (Willd.) Ching, Sunyatsenia 5: 250. 1940. *Polypodium subincisum* Willd. Sp. Pl. 5: 202. 1810. *P. sloanei* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 207 (seors. 55). 1849 (not *P. sloanei* Poepp. ex Spring. 1827). *Phegopteris subincisa* (Willd.) Fée, Gen. Fil. 243. 1852. *Dryopteris subincisa* (Willd.) Urban, Symb. Antill. 4: 19. 1903. *Aspidium subincisum* (Willd.) Christ, Bull. Herb. Boissier II. 6: 56. 1906.

In forests, often on sandy banks of ravines, 350-2,700 m.; Alta Verapaz; Izabal (?); Quezaltenango; San Marcos; Suchitepéquez (?). West Indies; southern Mexico; Honduras; Nicaragua to Colombia and Venezuela; Ecuador; Bolivia.

Plants terrestrial, often subarborescent, with stems to 0.5 m. tall; leaves to 2.5 m. long and over 1 m. broad; petiole to 0.7 m. long and 1 cm. in diameter, dark brown, abundantly (at base) provided with lustrous, dark-brown, lax, linear scales, these with conspicuously spinulose-dentate or denticulate margins, the teeth often minutely bifid at the tips, most of the cells many times longer than broad; lamina commonly 2-pinnate-pinnatifid, or rarely nearly 3-pinnate-pinnatifid as to enlarged basal pinnae, firm-membranaceous to chartaceous, deltoid or deltoid-ovate, tissue eglandular or essentially so, minutely strigose on both sides, especially on veins and margins; rachis gray- to yellow-brown, this and the costae provided abaxially with patent, filiform, reddish brown, dentate or denticulate scales, adaxially strigose, the trichomes similar to typical "*Ctenitis*-hairs," but longer and not as conspicuously articulate; pinnae spreading to ascending, lower ones short-petiolulate, basal ones basiscopically enlarged and more highly dissected; pinnules sessile, commonly deeply pinnatisect, or occasionally, in larger ones of lower pinnae, short-stalked and pinnate-pinnatifid; ultimate (tertiary) segments subfalcate, obtuse, entire to deep-crenate (rarely again pinnatifid), midrib of basal adnate segment commonly springing from junction of costa and costule, or from costa itself; veins 6-7 pairs in a segment, commonly 1- to 3-forked, the branch tips terminating in hydathodes well short of the margin; sori medial, or rarely inframedial, borne on the vein or the acroscopic branch, exindusiate.

This and *C. pulverulenta* and the Antillean *C. villosa* (L.) Copel. form a closely knit species complex. All are provided with narrow, dentate or denticulate scales, and all have the apices of segments very broadly rounded. Leaves of *C. subincisa* are essentially bipinnate-pinnatifid (above the more highly dissected basal pinnae) and are not nearly as huge as the 3- to 4-pinnate leaves of the other two species. Of the three, only *C. villosa* has indusiate sori. All exhibit some dif-

ferences in the amount and placement of indument. *Ctenitis villosa* and the typical variety of *C. pulverulenta* are abundantly pilose on the surfaces and margins of segments, while in *C. pulverulenta* var. *heydei* they are essentially glabrous. *Ctenitis subincisa* is intermediate in this character, with less conspicuous trichomes occurring on the midribs and segment margins. Taxonomy of the complex needs more careful examination.

Ctenitis submarginalis (Langsd. & Fisch.) Ching, Sunyatsenia 5: 250. 1940. *Polypodium submarginale* Langsd. & Fisch. Icon. Fil. 12, t. 13. 1810. *P. caripense* Willd. Sp. Pl. 5: 202. 1810. *Aspidium caripense* (Willd.) Mett. Fil. Hort. Lips. 90, t. 18. 1856. *Nephrodium caripense* (Willd.) Hook. in Hook. & Bak. Syn. Fil. 265. 1867. *Ctenitis submarginalis* f. *caripensis* (Willd.) Lell. Proc. Biol. Soc. Wash. 89: 710. 1977.

Known thus far in Guatemala from one collection: 1,350 m., Cobán, Alta Verapaz, 1908 (*Tuerckheim II-1204*). Hispaniola; southern Mexico; Honduras; Nicaragua to Colombia and Venezuela, south to Argentina and Uruguay.

Plants terrestrial; rhizome erect to ascending, apex densely covered with lustrous, orange, translucent scales, these to 2 cm. long, linear or linear-lanceolate, attenuate, lax, flattened but often twisted, entire to remotely and minutely denticulate, the bases flat or slightly revolute; leaves fasciculate, mature ones 0.3-1 m. long, 0.2-0.3 m. broad; petiole 24-50 cm. long, nearly as long as the lamina, yellowish to light brown, abundantly provided with orange or light-brown scales, to about 8 mm. long, similar in shape and character to those of the rhizome; lamina pinnate-pinnatifid, firm-membranaceous, ovate, abruptly narrowed to a pinnatifid apex, not or slightly glandular, margins and both sides of leaf surface sparsely provided with minute, septate trichomes; rachis stramineous to light brown, amply provided with scales as on the petiole, and with short, septate, trichomes adaxially; pinnae spreading to ascending, subdistant, sessile, or lower ones short-stalked, oblong-lanceolate, acuminate, truncate at base, cut halfway or nearly quite to the costa; costa densely septate-pubescent adaxially, the abaxial side provided with scales like those of the main axis, only much smaller; ultimate segments subentire, falcate, commonly rounded or subtruncate at apex, often appearing acute due to the folded margins, sometimes truly acute, and very rarely apiculate; veins 8-15 pairs (in larger segments), simple, terminating at or very near the margin; sori one to a vein throughout the segment, medial to supramedial between midrib and segment margin; indusium fugacious, usually small and inconspicuous, light or reddish brown, essentially eglandular, margins subentire, erose or with a few, short cilia.

The species is not very common in Central America, being represented by one to several collections in each of the countries in which it has been found. Occurrence in South America (especially Brazil) is more frequent, where perhaps it may vary infraspecifically. Christensen (1913) suggested that six rather local forms might be recognized throughout the range.

EXCLUDED SPECIES

Dryopteris tonduzii (Christ) C. Chr. Index Fil. 664. 1906. *Aspidium tonduzii* Christ, Prim. Fl. Costaric. 3: 34. 1901.

Christensen (1920) cited *Heyde & Lux* (ed. Donn.-Sm. 4425) from Santa Rosa as *D. tonduzii*. However, close examination of this collection and comparison with type material reveals that it is *Ctenitis nigrovenia*. The two species are very closely related and may be easily confused, but can be distinguished by characteristics of the indusium and scales. In the latter, indusia are minute, dark reddish brown, and very early fugacious, and scales of the rachis are linear to filiform, with an expanded, often subbullate base. *Dryopteris tonduzii*, from Nicaragua and Costa Rica, has relatively large, usually lighter brown, subsistent indusia, and rachis scales are broader (linear-lanceolate to ovate) and tend to be flattened and not particularly expanded at base.

CYCLOPELTIS J. Smith

Plants of medium size, terrestrial, erect; rhizome stout, commonly suberect, scaly; leaves monomorphic, coarse, erect, rather scaly on main axes; petiole not articulate at the rhizome; lamina 1-pinnate, narrowed to both ends; rachis densely but minutely hispidulous on abaxial side; pinnae numerous, articulate at the rachis; venation anadromous, the veins free, pinnately branched; sori abaxial on the veins; indusia peltate, commonly fugacious, dark brown to blackish on dried specimens, essentially glabrous; sporangia long-stalked; spores monolete, bilateral, with perine, surface irregularly tuberculate.

This is a small genus, consisting of three to six similar species. Old World representatives are found from Burma and Malaysia and the Philippines. One species occurs in the neotropics.

Cyclopetlis semicordata (Sw.) J. Sm. Bot. Mag. 72: Compan. 36. 1846. *Polypodium semicordatum* Sw. Prodr. 132. 1788. *Polystichum semicordatum* (Sw.) Moore, Index Fil. lxxxiv. 1857.

In deep, wet forests, commonly at bases of trees or along stream banks, sometimes atop rocky banks, sea level to 400 m.; Alta Verapaz; Esquintla; Izabal; Petén; Rehahuleu. West Indies; southern Mexico to Panama; Colombia to the Guianas, and south to Brazil and Bolivia.

Rhizome stout, suberect or decumbent, densely covered with orange or light-brown scales, these linear or linear-lanceolate, attenuate; leaves several, fasciculate, to 1.5 m. long and 0.25 m. broad; petiole short, subterete, rounded abaxially, sulcate adaxially, amply provided with brown, linear, attenuate scales; lamina firm-membranaceous to chartaceous, oblanceolate, pinnate, reduced at both ends, the apical segment similar in shape and size to the distal pinnae; rachis densely hispidulous (abaxially) with stout but

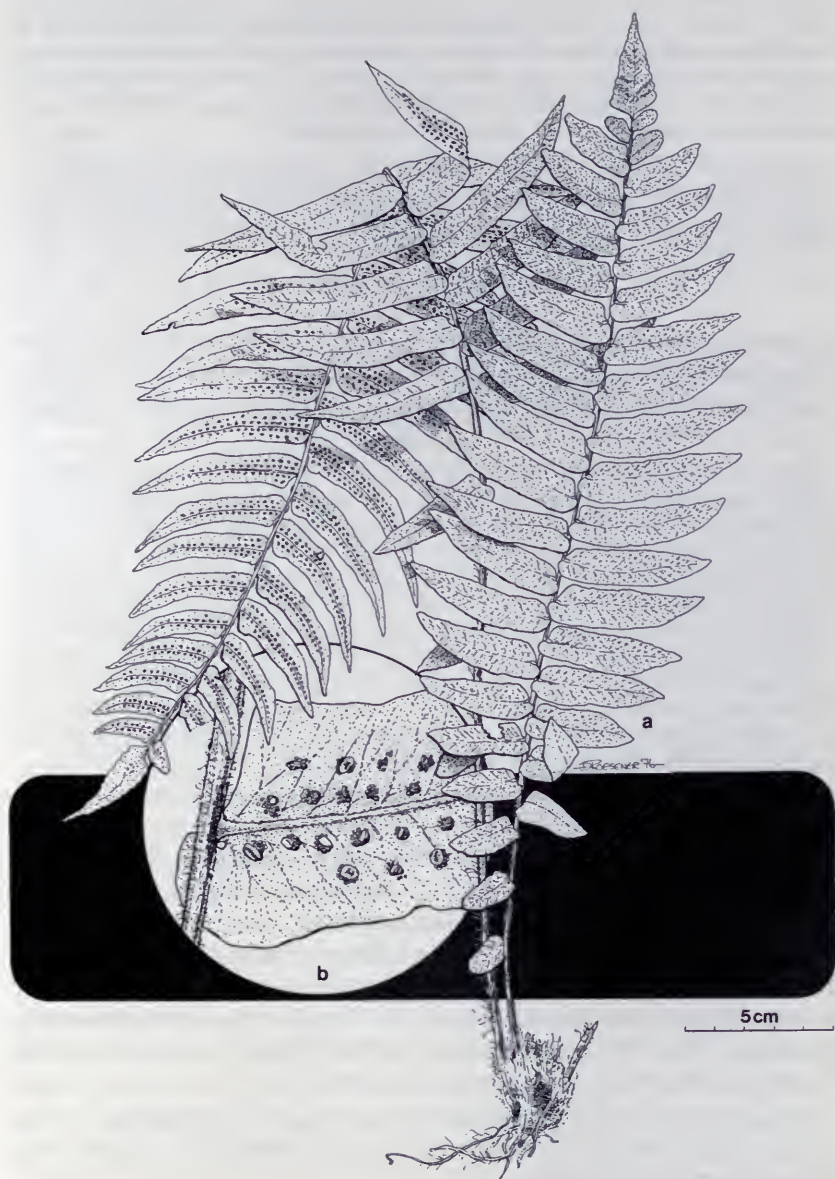


FIG. 20. *Cyclopeltis semicordata*. a, habit, $\times \frac{1}{2}$; b, portion of rachis and pinna base.

minute trichomes, and also provided with scattered, brown scales; pinnae numerous, sessile, glabrous, to 12 cm. long and 2 cm. broad, articulate at the rachis and spreading from it at nearly right angles, subentire to undulate-crenate, acuminate, truncate to subcordate-auriculate at base, the auricle produced basiscopically and usually overlapping the adaxial side of the rachis; veins free, pinnately 2- to 4-branched from the costa; sori round, borne on vein branches, in 1-3 (commonly 2) rows on each side of the costa, the double line generally nearer the costa than the margin.

Many Old World specimens are found in herbaria annotated as *C. semicordata*, for the genus was once considered monotypic. But there are at least three good species of *Cyclopeltis*, probably more.

CYRTOMIUM Presl

REFERENCES: L. M. Underwood, American ferns II. The genus *Phanerophlebia*, Bull. Torrey Bot. Club 26: 205-216. 1899. C. V. Morton, Observations on cultivated ferns II. The proper generic name of the Holly Fern, Amer. Fern J. 47: 52-55. 1957.

Plants of medium to large size, terrestrial, erect; rhizome stout, erect or ascending, scaly; leaves essentially monomorphic, erect; petiole scaly (at least near the base), not articulate; lamina firm-textured, often coriaceous or subcoriaceous, pinnate, with a conform or subconform terminal pinna (in ours) or rarely reduced to a pinnatifid apex, not or scarcely reduced at base, the axes amply to sparsely provided with brown, often hairlike scales, essentially lacking trichomes; pinnae few or (commonly) numerous, acute to acuminate or attenuate, rarely obtuse, often falcate or subfalcate, the margin commonly cartilaginous and serrate, especially toward the apex, the serrations terminating in rigid, antrorse spines; venation anadromous, pinnately branched, free, or the vein branches anastomosing toward the margin; sori round, abaxial, borne on the branches of veins; indusium peltate, sometimes persistent, but more commonly fugacious and thus apparently lacking; sporangia long-stalked; spores monolete, bilateral, with perine.

The genus was separated by Presl into two genera, primarily on the basis of free *vs.* anastomosing veins. However, this character is highly variable and is uncorrelated with any other significant features. Although Copeland united the two in his *Genera Filicum* (1947) under *Phanerophlebia*, Morton (1957) indicated that they had been already properly united under *Cyrtomium* by Moore (*Index Filicum* LXXXII, 1857). *Cyrtomium*, thus delineated, contains about 20 species rather evenly divided between the Old and the New World. American species are found from the southwestern United States to northern South America, with one in the Greater Antilles.

A few of the Asian species are quite popular in cultivation in the United States. They are hardy and easy to grow and are especially desired for terrarium use.

a. Veins regularly anastomosing toward pinna margin.

b. Pinnae 3-12 (15); inner line of sori near (1-2 mm.) or crowding the costa.
C. juglandifolium.

- b. Pinnae (12) 14-30; inner line of sori subdistant (3-5 mm.) from the costa. *C. remotisporum*.
- a. Veins essentially free, rarely or never anastomosing.
- c. Pinnae 2-7 (9), rarely more than 6 cm. long and 2 cm. broad, rounded or cordate at base. *C. pumilum*.
- c. Pinnae numerous, larger ones 15-27 cm. long and 2.5-3.8 cm. broad, cuneate at base. *C. macrosorum*.

Cyrtomium juglandifolium (H. & B.) Moore, Index Fil. LXXXIII.

1857. *Polypodium juglandifolium* H. & B. in Willd. Sp. Pl. 5: 195.

1810. *Aspidium juglandifolium* (H. & B.) Kunze, Linnaea 20: 363.

1847 (not D. C. Eaton, 1880). *Phanerophlebia juglandifolia* (H. & B.)

J. Sm. J. Bot. (London) 4: 187. 1842.

In wet forests or thickets, on slopes or in ravines, often along streams, 800-3,100 m.; Alta Verapaz; Escuintla; Huehuetenango; Quezaltenango; El Quiché; San Marcos. Southern Mexico; El Salvador; Nicaragua to Colombia and Venezuela.

Leaves several, caespitose, to 80 cm. tall and 25 cm. broad; petiole to 40 cm. long, rounded abaxially, sulcate adaxially, near the base amply provided with brown scales, these lanceolate to ovate, often attenuate, their margins usually obscurely dentate; lamina firm-herbaceous to subcoriaceous, ovate or broadly lanceolate, pinnate, the apical pinna long-stalked, otherwise similar to the lateral ones; rachis sparsely provided with light- to dark-brown, tortuous, often hairlike scales, and frequently bearing a scaly, proliferous bud at the axil of the uppermost lateral pinna; pinnae 3-12 (15), remote, lanceolate, subfalcate, short-stalked, rounded to cuneate at base, attenuate at apex, glabrous, but with hairlike scales widely scattered on the costa and veins abaxially, larger ones 9-16 (20) cm. long and (1.5) 2-4.5 cm. broad; veins 2- to 3-branched, commonly raised and distinct, the more distal branches regularly anastomosing with those of adjacent veins; sori 2- to 3-seriate between costa and margin, the inner line very near and often crowding the costa; indusia 0.5-1.8 mm. in diameter, fugacious or apparently lacking.

The differences between this and *C. remotisporum* are quantitative and not particularly substantial. The two taxa historically have been separated on the basis of the comparative proximity of the inner soral line and number and size of pinnae. Throughout the combined range of both (southern Mexico to Venezuela) there appears to be a trend from more and narrower pinnae in the north to fewer and broader pinnae toward the south, and this seems to be loosely correlated with soral lines borne further from the costa in the narrower pinnae. But with the lack of further substantiating features, this hardly should merit more than infraspecific delimitation. For purposes of this treatment, I have adapted Underwood's rather arbitrary measurement of the distance of inner soral line from the costa as 3-5 mm. for *C. juglandifolium* vs. 2 mm. for *C. remotisporum*. However, in a number of specimens of the latter, sori are either underdeveloped or past maturity with many

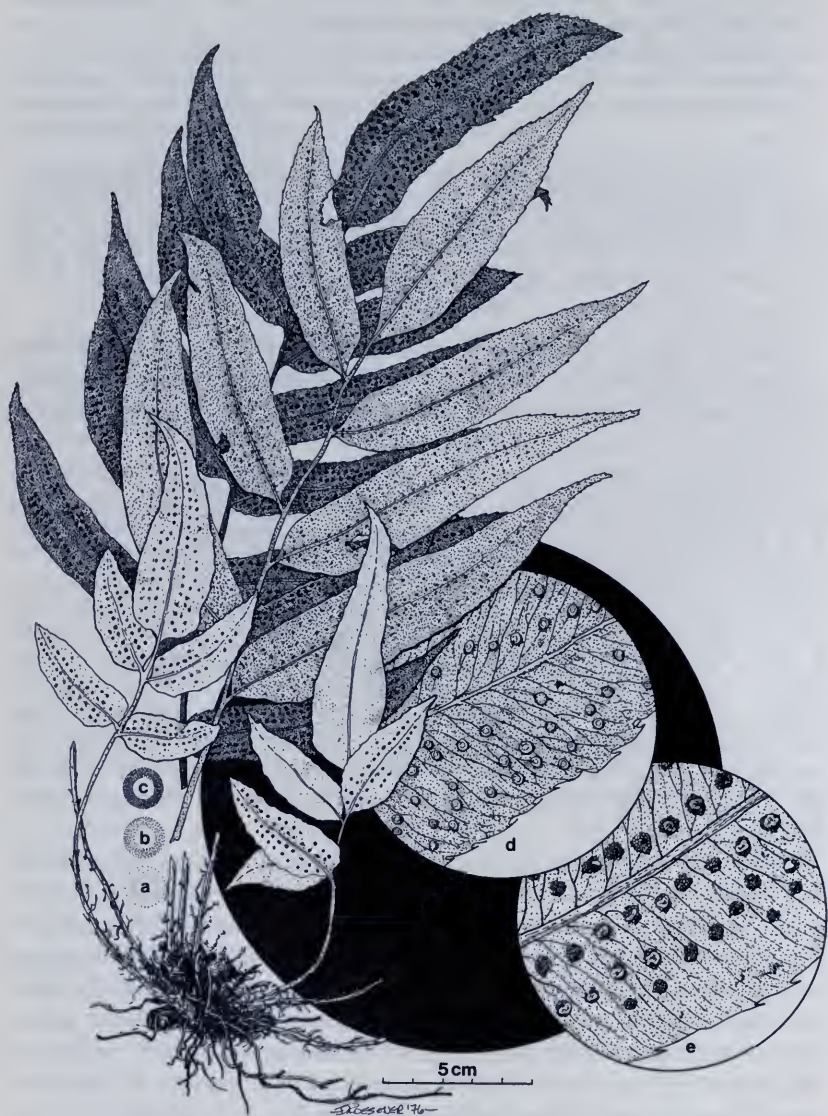


FIG. 21. *Cyrtomium*. a, *C. pumilum*, habit, $\times \frac{1}{2}$; b, *C. juglandifolium*, habit, $\times \frac{1}{2}$; c-d, *C. remotisporum*: c, habit, $\times \frac{1}{2}$; d, portion of pinna with sori, $\times 2$; e, *C. macrosorum*, portion of pinna with sori, $\times 2$.

sporangia fallen away; and if these had been examined in full size during maximum development, they certainly would have appeared to have been much closer to the costa. A conclusion as to whether the two taxa are good species or merely incipient ones perhaps may be determined in the future through field or greenhouse studies.

Cyrtomium macrosorum (Baker) Morton, Amer. Fern J. 47: 55. 1957. *Aspidium juglandifolium* var. *macrosorum* Baker, J. Bot. 25: 25. 1887. *Phanerophlebia macrosora* (Baker) Underw. Bull. Torrey Bot. Club 26: 213. 1899. *P. guatemalensis* Underw. *tom. cit.* 214. *Cyrtomium guatemalense* (Underw.) Morton, Amer. Fern J. 47: 55. 1957.

In wet, usually dense forests, on slopes or banks of ravines, often near streams, 1,800-2,800 m.; Chimaltenango; Huehuetenango; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Suchitepéquez. Southern Mexico; Nicaragua; Costa Rica; Panama.

Leaves several to many, caespitose, to 1.5 m. tall and 0.4 m. broad; petiole to 0.7 m. long, rounded abaxially, sulcate adaxially, amply or densely provided (at least on the proximal half) with light- to dark-brown scales, these lanceolate to ovate, often attenuate, their margins dentate or sparsely fimbriate; lamina chartaceous to subcoriaceous, oblong-lanceolate or -ovate, pinnate, the apical pinna long-stalked, and similar to the lateral ones; rachis sparsely to amply provided with brown, tortuous, lanceolate to linear or often hairlike scales, lacking a proliferous bud; pinnae numerous, remote, lanceolate or linear-lanceolate, scarcely or not at all falcate, stalked (proximal ones to 1 cm.) throughout, cuneate and slightly subdimidiate at base, attenuate at apex, glabrous, but with hairlike scales scattered on the costa and veins abaxially, larger ones 15-27 cm. long and 2.5-3.8 cm. broad; veins 3- to 5-branched, commonly raised and distinct, free or very rarely a few casually anastomosing near the margin; sori 1-2.4 mm. in diameter, 2- to 4-seriate between costa and margin; indusia often fully covering the sori, but commonly fugacious.

In his treatment of the genus *Phanerophlebia*, Underwood based his new species *P. guatemalense* on the type and one other specimen, and he knew *P. macrosora* only from the type locality. The former was presumed to have slightly wider pinnae, with a few more vein branches, and smaller sori equally distributed over the pinnae in four rows. Sori of the latter were said to be much larger and in two to three rows somewhat back from the margin. The number of vein branches (and therefore of soral rows) can obviously be few or more, depending on the width of pinnae, a variable characteristic and of itself hardly justifying distinction of species. The type of *P. guatemalense* bears sori well past maturity, with most sporangia fallen away, whereas that of *P. macrosora* bears fully developed sori, many with indusia still intact. Naturally, sori of the latter are larger. In observing the many

collections currently available in herbaria, the natural variability of the above characteristics is evident. *Cyrtomium macrosorum* in Mexico appears to have somewhat narrower and more coriaceous pinnae (rarely broader than 2.5 cm.) than plants farther south in the range, but it is clear we have one (not two) good species.

Cyrtomium pumilum (Mart. & Gal.) Morton, Amer. Fern J. 47: 54. 1957. *Aspidium pumilum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 64. 1842. *Phanerophlebia pumila* (Mart. & Gal.) Fée, Gen. Fil. 282. 1852. *Aspidium juglandifolium* D. C. Eaton, Ferns North Amer. 2: t. 75. 1880 (not Kunze, 1847).

In crevices of cliffs, 2,400-3,700 m.; Huehuetenango. Southern Mexico.

Leaves several to many, densely caespitose, to 28 cm. tall and 12 cm. broad; petiole to 12 (15) cm. long, rounded or somewhat angular abaxially, sulcate adaxially, amply provided with light- or dark-brown scales, these often attenuate, their margins dentate or sparsely fimbriate, those near the rhizome ovate to lanceolate, those toward the lamina becoming tortuous and hairlike; lamina coriaceous or subcoriaceous, ovate or deltoid, pinnate (or very rarely simple), the terminal segment long-stalked, similar to but commonly larger than the pinnae; rachis provided with brown, hairlike scales, lacking a proliferous bud; pinnae 2-7 (9), remote, ovate to lanceolate, scarcely or not at all falcate, short-stalked, rounded to cordate and often dimidiate at base, obtuse to acute or acuminate at apex, essentially glabrous, but with minute, brown scales scattered on the abaxial side, to 6 (9) cm. long and 2 cm. broad; veins 3- to 4-branched, obscure, free, or very rarely a few casually anastomosing near the margin; sori 1-2 mm. in diameter, 1- to 2-seriate between costa and margin; indusia nearly covering the sori, the margin subentire to dentate or erose, commonly fugacious.

Typical *C. pumilum* is a small plant, to 20 cm. tall, with two to four pinnae, and a terminal segment similar in shape but considerably larger. Lateral pinnae are relatively short and broad (ca. 5 cm. \times 2 cm.), with apex obtuse to acute. However two atypical plants have been collected (*Steyermark 50055*, Huehuetenango; *Little & Sharp 9922*, Chiapas, Mexico) which are nearly 30 cm. tall and bear seven to nine pinnae. Lateral pinnae are longer and narrower, with acuminate, almost attenuate apices, and terminal pinnae are scarcely, if at all, larger than lateral ones. In all other respects these specimens have the typical aspect of *C. pumilum*.

Whereas the typical habitat of other Guatemalan species of *Cyrtomium* is the forest floor, that of *C. pumilum* is almost exclusively crevices of cliffs (most label data indicates "limestone"). Indeed it may be the relatively severe conditions of this ecological niche which have inhibited leaf growth in this species—smallest in the genus.

Cyrtomium remotisporum (Fourn.) Morton, Amer. Fern J. 47: 54. 1957. *Phanerophlebia remotispora* Fourn. Mex. Pl. 1: 100. 1872 (type from Orizaba, Veracruz, Mexico, *Bourgeau 2349*).

On wet, wooded slopes and ravines, often along streams and rivers, occasionally among rocks, 1,200-2,000 m.; Alta Verapaz; El Quiché. Southern Mexico.

Leaves several, caespitose, to 1 m. tall and 0.25 m. broad; petiole to 50 cm. long, rounded abaxially, sulcate adaxially, near the base amply provided with brown scales, these lanceolate to ovate, attenuate, their margins often obscurely dentate; lamina chartaceous to subcoriaceous, ovate or broadly lanceolate, pinnate (or very rarely simple), the apical pinna long-stalked, otherwise similar to the lateral ones; rachis sparsely provided with light-brown, tortuous, hairlike scales, lacking a proliferous bud; pinnae (12) 14-30, remote, lanceolate, subfalcate, short-stalked, rounded to cuneate at base, attenuate at apex, glabrous, but with hairlike scales scattered on the costa and veins abaxially, larger ones 9-14 (18) cm. long and 1.3-2.8 cm. broad; veins 2- to 3-branched, often obscure, the more distal branches regularly anastomosing with those of adjacent veins; sori 2- to 3-seriate between costa and margin, the inner line subdistant (usually 3-5 mm.) from the costa; indusia usually less than 1 mm. in diameter, fugacious or apparently lacking.

This is very similar to, and perhaps conspecific with, *C. juglandifolia*. For further comparison, see discussion of the latter.

CYSTOPTERIS Bernhardt

REFERENCE: R. F. Blasdel, A monographic study of the fern genus *Cystopteris*, Mem. Torrey Bot. Club 21: 1-102. 1963.

Plants delicate, terrestrial or epipetric; rhizome scaly, short-creeping with leaves crowded to approximate or long-creeping with leaves subdistant to remote; leaves monomorphous, erect to pendent, to 40 cm. long (in ours); petiole glabrous to sparsely scaly, stramineous, or dark brown at base, not articulate; lamina narrow-ovate to deltoid-lanceolate, chartaceous to (in ours) firm-herbaceous or membranaceous, 2- to 4-pinnatifid, in ours to 10 (12) cm. broad; pinnae 6 to many pairs, short-stalked to sessile, subdistant to crowded, the pinnules or segments anadromous; veins free, anadromous, pinnately arranged; sori abaxial on the veins, essentially round, commonly discrete; indusium proximally attached to the base of the receptacle, arching over the sorus, the apex and (most of the) margins free, hemispherical to ovate-lanceolate, subpersistent; sporangia stalked; spores bilateral, monolet, echinate to rugose, with perine.

Cystopteris is a small genus with worldwide distribution. Its 8-10 species are very closely related and some of them apparently readily hybridize, thus contributing to a confused taxonomy. According to Blasdel (1963) introgressive hybridization is common, and this has further heightened the confusion. Some of these problems are discussed below under *C. fragilis*.

Only two species are recognized in Guatemala.

- a. Leaves crowded on a short-creeping rhizome; leaf tissue opaque, more than 1 cell thick; pinnae and segments crowded to (more commonly) subdistant. . . . *C. fragilis*.
- a. Leaves subdistant on a long-creeping rhizome; leaf tissue commonly translucent, 1 (2) cells thick; pinnae and segments crowded to imbricate. *C. membranifolia*.

***Cystopteris fragilis* (L.) Bernh.** Neues J. Bot. 1 (2): 26, t. 2, f. 9. 1806. *Polypodium filix fragile* L. Sp. Pl. 1091. 1753. *P. fragile* L. Fl. Suecica ed. 2: 374. 1755. *nom. alt.* (Linnaeus's trinomial reduced to binomial apparently because of conflicting genders in the double specific name). *P. diaphanum* Bory, Voyage Iles Mers Afrique 1: 328. 1804. *Athyrium fragile* (L.) Sprengel, Anleit. Kenntn. Gewächse 3: 136. 1804. *C. fragilis* var. *mackayii* Lawson, Fern Fl. Canada 233. 1889. *C. diaphana* (Bory) Blasdell, Mem. Torrey Bot. Club 21: 47. 1963.

In woods or thickets, commonly in wet places on banks of ravines or rivers, or on moist, rock crevices or outcrops, 1,400-3,800 m.; Alta Verapaz; Chimaltenango; Chiquimula; Huehuetenango; Quezaltenango; San Marcos; Sololá; Totonicapán. Mexico; El Salvador; Nicaragua to Colombia and Venezuela, south to Brazil and Argentina; Greater Antilles; United States; Canada; Greenland; Iceland; Old World.

Rhizome short-creeping, amply provided at the apex with lustrous, light- or dark-brown, lanceolate or linear-lanceolate scales; leaves several, crowded, to 40 cm. long and 8 cm. broad; petiole shorter than the lamina, glabrous except for a few basal scales; lamina 2- to 3-pinnate, lanceolate or ovate-lanceolate, firm-herbaceous, commonly several cells thick, not translucent; rachis light brown to stramineous, narrow-alate near the apex, but otherwise free, this and the costae sparsely provided with very minute 1- or 2-celled trichomes; pinnae spreading to somewhat ascending, subdistant to (rarely) crowded, ovate or ovate-lanceolate; pinnules adnate (or the basal pair often short-stalked), subdistant to close, rarely crowded; ultimate segments rounded to emarginate or subacute, with veins fully reaching the segment tips or notches; indusium ovate to hemispherical, mostly covering the sorus until maturity, at which time it is reduced to a small, inconspicuous, proximal sheath, not or scarcely projecting over the top of the sorus.

In Blasdell's monograph of *Cystopteris* (1963) he has maintained *C. fragilis* and *C. diaphana* as distinct species, primarily on the basis that the latter has smaller indusia with shorter, broader cells, and that the veins terminate in the notches of emarginate segments. *Cystopteris fragilis* is presumed to have larger indusia with longer, narrower cells, and the veins terminating in segment teeth. By these features (and some other relating to sporangial stalk development and gametophyte margins) are these two "species" differentiated. In addition the author distinguishes a fertile hybrid, *C. diaphana* × *fragilis* (= *C. fragilis* var. *mackayii*). If (as Blasdell points out) there *has* been backcrossing between the hybrid and both parents, the number and character of



FIG. 22. *Cystopteris*. a-b, *C. fragilis*: a, habit, $\times \frac{1}{2}$; b, pinnule, $\times 12$; c, *C. membranifolia*, habit, $\times \frac{1}{2}$.

fertile intergrades have been practically infinite, for all degrees of intermediacy have been observed in Guatemalan specimens alone. For example, the "most obvious" character (veins directed into segment teeth as opposed to segment notches) may be found to be somewhat constant on a number of specimens, but an equal number of Guatemalan specimens have been found with both conditions frequently observed, even on adjacent segments of the same pinna. The same may be said concerning other characters, *e.g.*, the size of indusia and shape of cells.

It may be that *C. fragilis* and *C. diaphana* are more distinct in other regions throughout the range, but it is virtually impossible to distinguish between the two in our area. Therefore for purposes of this treatment, only *C. fragilis* is recognized.

Linnaeus's change of name from *Polypodium filix fragile* to *P. fragile* apparently was not designed merely to reduce a trinomial, for there are numerous cases where trinomials were retained (and subsequently hyphenated by authors to conform with the rules of nomenclature). In this case "*fragile*" agrees with *Polypodium* (both neuter), where "*filix*" (feminine) does not. For full explanation, see Weatherby (Rhodora 28: 131. 1926).

***Cystopteris membranifolia* Mickel, Amer. Fern J. 62: 93. 1972.**

On banks of streams, montane cloud forests on slopes of Tajumulco Volcano, 8-10 km. west of San Marcos, Dept. San Marcos, ca. 2,300 m. (L. O. Williams *et al.* 26960). Apparently known in Guatemala only from this collection, and in Mexico from Puebla, Veracruz, and Oaxaca (type from Distrito Teotitlán, ca. 7,000 ft. alt., by waterfall in cut-over woods, Mickel 4544).

Rhizome long-creeping, protruding 1-5 mm. beyond the newest leaf, provided with lustrous, ovate, orange to reddish brown scales; leaves subdistant or remote, to 30 cm. long and 6 cm. broad; petiole shorter than the lamina, glabrous except for a few scales near the base; lamina pinnate-pinnatifid to nearly 2-pinnate, lanceolate or ovate-lanceolate, thin-membranaceous, translucent, commonly only 1 cell thick; rachis stramineous or yellowish brown, commonly alate in the distal half, glabrous or essentially so; pinnae sessile or subsessile, spreading or slightly ascending, commonly crowded to imbricate, deltoid- or elliptic-lanceolate; pinnules (or segments) crowded; ultimate segments obtuse to acute, commonly dentate, with veins terminating in the teeth; indusia tiny, inconspicuous, fugacious.

DENNSTAEDTIA Bernhardt

REFERENCE: R. M. Tryon, A review of the genus *Dennstaedtia* in America, Contr. Gray Herb. 187: 23-52. 1960.

Plants terrestrial, erect; rhizome long-creeping, lacking scales, but sparsely to amply pubescent, the trichomes often pluricellular, frequently articulated; leaves subdistant, large, often huge, monomorphous, pubescent to glabrous, lacking scales; petiole not articulate, commonly quite long, smooth or rarely aculeate toward the base; lamina 1- to 4-pinnate, firm-herbaceous to chartaceous, often to 1 m. broad, tapering gradually to a pinnatifid apex; pinnae spreading (often at 90°) to ascending; veins free, forked to pinnately branched in each ultimate segment; sori marginal, terminal on the vein branches abaxially, in most species borne in or near the sinus formed by 2 adjacent segments; indusium cup- to purse-shaped, consisting of a true, inner indusium joined to an opposed outer half formed by a modified lobe of leaf tissue; paraphyses lacking (at least in ours); sporangia on slender stalks; spores trilete or (rarely) monolete, with or without perine.

Dennstaedtia is a genus with typically large (to quite huge) decom-pound leaves which are rather widely spaced along a creeping, non-scaly rhizome. Perhaps its closest relative in Guatemala is *Hypolepis*, under which see further discussion. A single species occurs in North America, with about 20 others in the neotropics, and perhaps 50 more in the paleotropics. The following species have been found in Guatemala.

- a. Axis of the penultimate segments adaxially bordered by a herbaceous wing, this basiscopically decurrent (as a herbaceous wing or raised rib) onto the axis of the next order below.
 - b. Pinnules with their basal segments obviously alternate and unequal, the basiscopic segment sharply ascending, the acroscopic one spreading and more strongly produced; lamina commonly rather lustrous on both sides; apices of ultimate segments mostly sharply and deeply dentate. *D. bipinnata*.
 - b. Pinnules (at least of central pinnae) with their basal segments subopposite and subequal, the basiscopic one not or slightly ascending; lamina commonly dull on both sides; apices of ultimate segments mostly shallowly and obtusely dentate. . . . *D. globulifera*.
- a. Axis of the penultimate segments not bordered by a herbaceous wing, or if so then the wing not decurrent onto the axis of the next order below.
 - c. Costules (and often tertiary axes) sparsely to densely pubescent abaxially (at least in Guatemala), the trichomes 0.3-1.0 mm. long, mostly spreading; vein tips on adaxial side of sterile segments slender, not or scarcely enlarged.
 - d. Pinnae opposite or subopposite, sessile or subsessile; proximal pinnae with basal pair of pinnules greatly reduced. *D. distenta*.
 - d. Pinnae alternate, at least the proximal ones short-stalked; proximal pinnae not or scarcely reduced at base. *D. cicutaria*.
 - c. Costules and tertiary axes glabrous to sparsely or minutely pubescent, the trichomes few or, if abundant, then short (0.1-0.2 mm.), curled, and appressed; vein tips (most of them) on adaxial side of sterile segments enlarged (very rarely slender in *D. dissecta*).
 - e. Lamina 2-pinnate to 2-pinnate-pinnatisect; soriferous ultimate segments entire to lobed, if lobed then the sori borne on the lobes (only rarely in the sinus between lobes). *D. arborescens*.
 - e. Lamina nearly 3-pinnate to 4-pinnate; soriferous ultimate segments lobed, the sori commonly borne in the sinus (only rarely on the lobes). *D. dissecta*.

Dennstaedtia arborescens (Willd.) Maxon, Proc. Biol. Soc. Wash. 43: 88. 1930. *Davallia arborescens* Willd. Sp. Pl. 5: 470. 1810. *D. concinna* Presl, Rel. Haenk. 1: 66. 1825 (not Schrad. 1818). *Dicksonia concinna* (Presl) Hook. Sp. Fil. 1: 74. 1844. *D. consanguinea* Kl. Linnaea 20: 445. 1847. *Dennstaedtia concinna* (Presl) Moore, Index Fil. xcvi. 1857. *D. consanguinea* (Kl.) Moore, op. cit. 305. 1861. *D. grossa* Christ, Bull. Herb. Boissier II. 6: 192. 1906.

This is apparently represented thus far in Guatemala by a single collection: Senahú, Alta Verapaz, 3,000 ft., *Hatch & Wilson 114*, 1936; elsewhere in wet forests or thickets, Southern Mexico to Panama; Greater Antilles; Venezuela; Colombia to Bolivia.

Leaves to 3 m. long and 1 m. broad; petiole dull brown, terete abaxially, sulcate adaxially, glabrous, or sparsely pubescent at base; lamina 2-pinnate to 2-pinnate-pinnatifid, chartaceous to subcoriaceous, not or scarcely lustrous, glabrous, or sparsely pubescent on the axes abaxially, the trichomes minute, subappressed, and commonly curled; rachis dull light or dark brown, smooth, terete abaxially, sulcate adaxially; pinnae short-stalked to sessile, slightly ascending; pinnules subentire to deeply pinnatifid, sessile or sessile, obtuse to acuminate, the lobes or segments (if any) commonly truncate or broadly rounded (rarely subacute) at apex, costules flush or slightly parallel-ridged adaxially, but the ridges (if any) not decurrent onto the costa; veins distinct, sometimes prominent adaxially, the sterile tips commonly enlarged and conspicuous, terminating short of the margin; sori borne regularly along the margin of pinnules, or along the margins of unlobed segments, or on the lobes of segments (only rarely in the sinus between lobes); indusium shallowly or deeply cup-shaped (hemispherical) to purse-shaped (somewhat broader than long).

As is common with ferns having huge leaves, collections of this species are often carelessly made and annotated. Thus a herbarium sheet may contain only a pinna or pinnule (this often mounted without the axis on which it was borne), and lack label data as to whether this is a secondary or tertiary division. In these cases some pinnae of *D. arborescens* may closely resemble pinnules of *D. dissecta* with broad segments.

Dennstaedtia bipinnata (Cav.) Maxon, Proc. Biol. Soc. Wash. 61: 39. 1938. *Dicksonia bipinnata* Cav. Descr. 174. 1802. *Dicksonia adiantoides* Willd. Sp. Pl. 5: 488. 1810. *Dennstaedtia adiantoides* (Willd.) Moore, Index Fil. xcvi. 1857.

In montane rain forests, often on ridges and slopes, 1,300-1,900 m.; San Marcos; Santa Rosa. Southern Florida; Mexico to Panama; Greater Antilles; Trinidad to Colombia; Ecuador; Peru; Bolivia.

Leaves to 3 m. long and 1 m. broad; petiole stramineous to dark brown, always darkest at the base, terete abaxially, sulcate adaxially, glabrous or, toward the base, sparsely to amply provided with reddish brown, appressed, pluricellular trichomes; lamina 3-pinnate-pinnatifid to 4-pinnate, firm-herbaceous to subcoriaceous, often rather

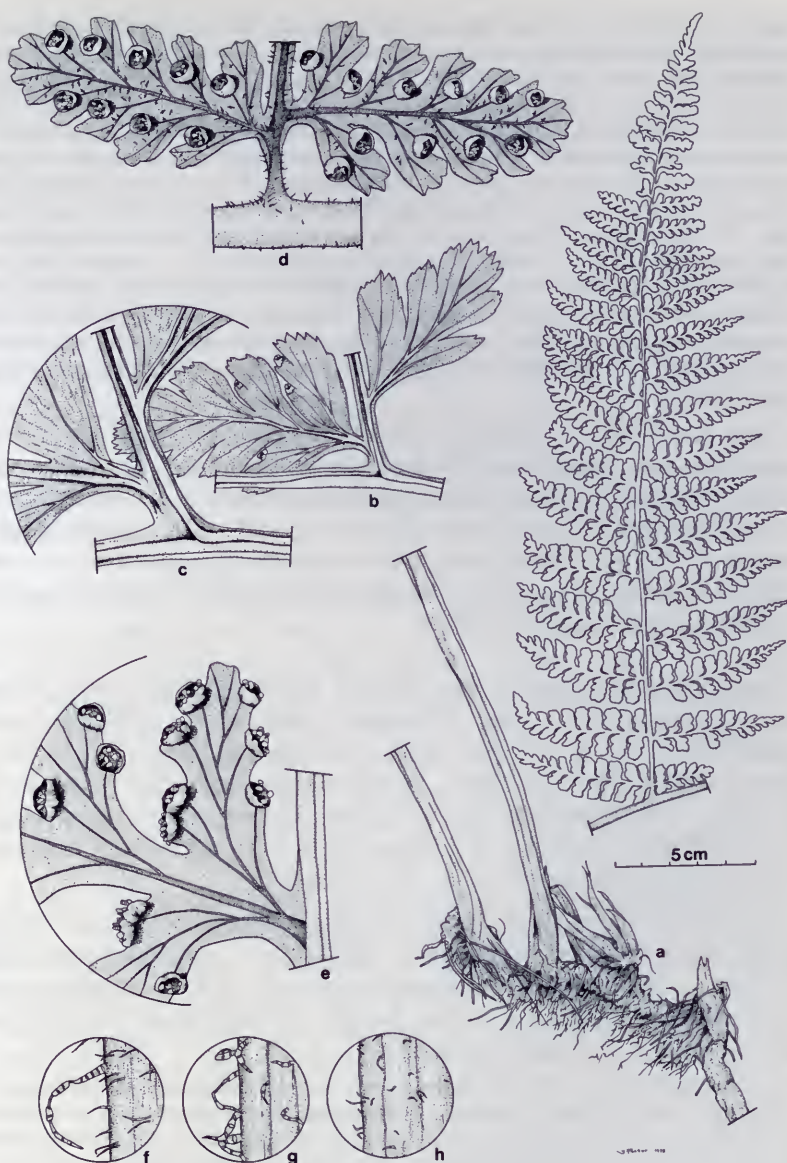


FIG. 23. *Dennstaedtia*. a, *D. dissecta*, habit, rhizome, and one pinna, $\times \frac{1}{2}$; b-c, *D. bipinnata*: b, ultimate segments and sori, adaxial side, $\times 3\frac{1}{2}$; c, configuration of axes, adaxial side, $\times 7$; d, *D. globulifera*, ultimate segments and sori, abaxial side, $\times 3\frac{1}{2}$; e, *D. dissecta*, ultimate segment and sori, abaxial side, $\times 7$; f, *D. cicutaria*, portion of costa with two kinds of trichomes, $\times 25$; g, *D. distenta*, portion of costa with trichomes, $\times 25$; h, *D. dissecta*, portion of costa with trichomes, $\times 25$.

lustrous on both sides, sparsely pubescent abaxially or glabrate; rachis stramineous to light brown, somewhat lustrous, smooth, terete abaxially, sulcate adaxially, glabrous, or provided with a few, minute reddish brown trichomes; pinnae stalked, ascending, crowded to imbricate, inequilateral at base (several proximal pinnules more strongly produced acroscopically than basiscopically); pinnules mostly stalked, subdeltoid to ovate or lanceolate, acute to acuminate, with their basal segments obviously alternate and unequal (the basiscopic segment sharply ascending, the acroscopic one spreading and more strongly produced); costules adaxially bordered by a raised rib or herbaceous wing, this basiscopically decurrent onto the axis of the next order above or below; ultimate segments lobed or dentate, the apices laciniate to acutely or subacutely dentate; veins distinct, often prominulous adaxially, the sterile tips slender to slightly thickened, commonly terminating short of the margin; sori commonly borne in the sinus between lobes of acroscopic segments or, less often, on a smaller lobe above the sinus; indusium broadly cylindrical to subglobose, commonly as long as or longer than broad (only rarely broader than long).

This is apt to be confused with *D. globulifera*, especially where collections are represented by incomplete specimens. Care must be taken to examine features on comparable portions of the lamina. For example, relative size and orientation of segments may be quite consistent on central pinnae, but may differ considerably compared to those of basal or apical pinnae. This is discussed in detail by Tryon on page 38 of his review of the genus (1960).

Dennstaedtia cicutaria (Sw.) Moore, Index Fil. xcvi. 1857. *Dicksonia cicutaria* Sw. J. Bot. (Schrader) 1800 (2): 91. 1801. *D. rubiginosa* Kaulf. Enum. Fil. 226. 1824. *Dennstaedtia rubiginosa* (Kaulf.) Moore, Index Fil. xcvi. 1857. *Dicksonia decomposita* Christ, Bull. Soc. Roy. Bot. Belgique 35: 180. 1896. *Dennstaedtia decomposita* (Christ) Christ, Bull. Herb. Boissier II. 5. 732. 1905. *Cola de chum-pipe* (Huehuetenango, *vide* J. A. Steyermark).

In forests, thickets, or wooded ravines, occasionally in open areas along banks of rivers or streams, 450-2,000 m.; Alta Verapaz; Baja Verapaz; Guatemala; Huehuetenango; Izabal; Quezaltenango; Suchitepéquez. Greater Antilles; Mexico to Colombia and Venezuela, and southward to Brazil and Bolivia.

Leaves to 3.5 m. long and 1 m. broad; petiole dull yellowish brown to dark brown, always dark brown at base, terete abaxially, sulcate adaxially, glabrous, or sparsely pubescent at base; lamina 3-pinnate to 4-pinnate-pinnatifid, firm-herbaceous to chartaceous, sparsely to (more commonly) densely pubescent, especially abaxially; rachis dull yellowish or darker brown, smooth, terete abaxially, sulcate adaxially, minutely (often densely) puberulent; pinnae alternate, mostly short-stalked, ascending, not or scarcely reduced at base; pinnules sessile to short-stalked, spreading from the costa at broad (often 90°) angles; costae and costules sulcate adaxially, amply to abundantly pilose (especially abaxially), the trichomes usually of 2 kinds, most of them 0.3-1.0 mm. long,

rather rigid, slightly curved, spreading, pluricellular, their cells mostly much longer than broad, these mixed with shorter, unicellular, acicular ones; axis of the penultimate segments shallowly sulcate adaxially, but the parallel ridges not decurrent onto the axis of the next order below; ultimate segments commonly dense-pilose, especially abaxially, the rigid trichomes borne on midrib and veins and often on the tissue between the veins; veins commonly rather distinct, those of sterile segments with tips slender, not or scarcely enlarged adaxially, terminating well short of the margin; sori borne usually at the sinuses between segment lobes; indusia shallowly to deeply cup-shaped, commonly hemispherical, but frequently somewhat broader than long.

This and *D. distenta* are very similar and can be rather easily distinguished from other Guatemalan species by the conspicuous pubescence of the axes and from each other by the character of this pubescence. (See treatment of the former for further discussion.) Also, besides the features noted in the key, *D. cicutaria* may be further separated from *D. distenta* by the position of the sori. In the former, the sorus is most commonly borne in the sinus between two segment lobes, but in the latter usually at the end of a small acroscopic (occasionally basiscopic) lobe of the segment.

Dennstaedtia dissecta (Sw.) Moore, Index Fil. 305. 1861. *Polypodium dissectum* Sw. Prodr. 134. 1788 (not Forst. 1786). *Dicksonia obtusifolia* Willd. Sp. Pl. 5: 483. 1810. *D. ordinata* Kaulf. Enum. Fil. 226. 1824. *D. cornuta* Kaulf. tom. cit. 227. *Dennstaedtia obtusifolia* (Willd.) Moore, Index Fil. 306. 1861. *D. ordinata* (Kaulf.) Moore, loc. cit. *Dicksonia cicutarioides* Fée, Mém. Fam. Foug. 11: 94. 1866 (not *D. cicutaria* Sw. 1801). *Dennstaedtia cicutarioides* (Fée) Hieron. Bot. Jahrb. Syst. 34: 454. 1904 (not *D. cicutaria* [Sw.] Moore, 1857). *D. cornuta* (Kaulf.) Mett. Ann. Sci. Nat. Bot. V. 2: 260. 1864.

In wet forests or thickets, often on banks of shaded ravines, 100-2,500 m.; Alta Verapaz; Izabal; Quezaltenango; San Marcos; Santa Rosa; Suchitepéquez. West Indies; Southern Mexico to Panama; Trinidad to Colombia, south to Brazil and Bolivia.

Leaves to 3 m. long and 1 m. broad; petiole dull brown, terete abaxially, sulcate adaxially, glabrous, or sparsely pubescent at base; lamina nearly 3-pinnate to 4-pinnate, firm-herbaceous to chartaceous, not or scarcely lustrous, glabrous to pubescent on the axes, the trichomes minute, subappressed and commonly curled; rachis dull, stramineous to brownish, terete abaxially, sulcate adaxially; pinnae sessile or subsessile, spreading to slightly ascending; pinnules (at least on proximal pinnae of mature leaves) fully pinnate to nearly 2-pinnate, sessile or subsessile, subacute to acuminate; costules with or without raised parallel ribs or herbaceous wings adaxially, if so then the wings or ribs not decurrent onto the axis of the next order above or below; ultimate segments lobed, often deeply so, glabrous, or minutely pubescent abaxially; veins distinct, the sterile tips mostly enlarged and conspicuous, terminating short of the margin; sori

commonly borne in the sinuses of segment lobes, or rarely on a smaller lobe just above the sinus; indusia 0.5-1.5 mm. broad, shallowly or deeply cup-shaped (hemispherical) or purse-shaped (somewhat broader than long).

In the past, this has been provisionally separated from *D. obtusifolia* on the basis of relative size and shape of sori. However, sori in this species complex vary to the same degree as size and shape of ultimate segments, all of which are probably affected by the degree of maturity of leaves or by type of habitat. In the many collections I have examined from the neotropics there appears to be no real consistency in this feature, as some sori are often hemispherical and small on some segments and elongated and larger on others (or they even differ on the same segment).

Dennstaedtia dissecta is most closely related to *D. arborescens*, under which see further discussion.

Dennstaedtia distenta (Kunze) Moore, Index Fil. 306. 1861. *Dicksonia distenta* Kunze, Analect. Pterid. 39. 1837 (type from Jalapa, Mexico, *Schiede s.n.*). *Dennstaedtia mexicana* Rosenst. nom. illeg.

In wet forests or thickets, on slopes or along streams, frequently in sandy soil, 1,700-2,800 m.; Alta Verapaz; Chimaltenango; Quezaltenango; San Marcos; Zacapa. Mexico to Panama; Hispaniola; Jamaica.

Leaves to 2.5 m. long and 1 m. broad; petiole smooth, dull, stramineous or yellowish brown, usually darker at base and here occasionally sparsely pubescent and aculeolate, terete abaxially, sulcate adaxially; lamina 3- to 4-pinnate-pinnatifid, thin- to firm-membranaceous, glabrate to (in ours) amply or densely pubescent, especially abaxially; rachis terete to subquadrangular and stramineous abaxially, sulcate and stramineous to yellowish brown adaxially, minutely pubescent to glabrate; pinnae opposite or subopposite, sessile, spreading (often at a 90° angle) to slightly ascending, greatly reduced at base; pinnules sessile or subsessile, spreading from the costa at broad (often 90°) angles, the basal pair appreciably to greatly reduced; costae and costules sulcate adaxially, amply to abundantly villous (at least in ours), the trichomes predominantly of one kind, 0.3-0.5 mm. long, subappressed to spreading, rather lax, often tortuous, pluricellular, articulate (and frequently moniliform), their cells 1-2 times as long as broad; axis of the penultimate segments flush or slightly parallel ridged adaxially, but the ridges (if any) not decurrent onto the axis of the next order below; ultimate segments glabrate, or (more commonly) amply to sparsely villous along the midrib and veins; veins commonly distinct, those of sterile segments with tips slender, not or scarcely enlarged adaxially, terminating well short of the margin; sori borne usually on acroscopic (or occasionally basiscopic) lobes of ultimate segments; indusium shallowly or deeply cup-shaped (hemispherical) or, less often, purse-shaped (somewhat broader than long).

This and *D. cicutaria* are closely related, and both can be distinguished from other Guatemalan species not only by the slender (rather than enlarged) sterile vein tips on the adaxial surface, but also by the spreading, rather conspicuous pubescence (to 1 mm.) of axes and

veins. Other species are glabrous, or sparsely or very minutely pubescent, with trichomes usually appressed. Trichomes on the axes (and often veins) in *D. distenta* are rather lax, often tortuous, articulate (frequently moniliform), the many cells about as long as or slightly longer than broad. Those of *D. cicutaria* are usually of two kinds, intermixed; one kind shorter, rigid, and acicular, with 1-3 cells, the other longer, similar to those of *D. distenta*, but more rigid, terete to somewhat articulate, the many cells several to many times as long as broad. This difference in types of trichomes is subtle, but quite consistent, and serves as another means of separating the two species. Tryon (1960, p. 36) mentions a glabrate variant of *D. distenta* found in Jamaica and Hispaniola which has perhaps more constricted segments, which may or may not warrant distinction. However, all the specimens in Central America which I have examined are rather consistently villous, at least on the midribs and axes of segments abaxially.

Dennstaedtia globulifera (Poir.) Hieron. Bot. Jahrb. Syst. 34: 455. 1904 (not *D. globuligera* Desv. 1827). *Polypodium globuliferum* Poir. Lam. Encycl. 5: 554. 1804. *Dicksonia exaltata* Kunze, Bot. Zeit. 8: 59. 1850. *D. globulifera* (Poir.) O. Ktze. Rev. Gen. Pl. 3 (2): 378. 1898. *Dennstaedtia exaltata* (Kunze) Hieron. Bot. Jahrb. Syst. 34: 454. 1904.

In montane rain forests and in wooded ravines, often on slopes or on banks of streams, 600-2,300 m.; Alta Verapaz; Chimaltenango; Sacatepéquez; San Marcos; Santa Rosa. Mexico to Panama; Greater Antilles; Venezuela and Colombia to Brazil and Argentina.

Leaves to 3 m. long and 1 m. broad; petiole yellowish to dark brown, always darkest at base, terete abaxially, sulcate adaxially, glabrous to sparsely pubescent distally, or abundantly so at base, the trichomes appressed to spreading, reddish brown, pluricellular; lamina 3-pinnate to nearly 4-pinnate, thin- to firm-herbaceous, not or scarcely lustrous, glabrous or sparsely pubescent; rachis stramineous to light brown, not or scarcely lustrous, smooth, terete abaxially, sulcate adaxially, glabrous or with a few scattered, reddish brown trichomes; pinnae sessile to short-stalked, spreading to ascending, contiguous to imbricate, subequilateral at base (or the basal pinnules slightly longer acroscopically than basiscopically); pinnules sessile to short-stalked, lanceolate or deltoid-lanceolate, subacute to acuminate, at least those of the central pinnae with their basal segments subopposite and subequal (the basiscopic one not or slightly ascending); costules adaxially bordered by raised, parallel ribs or herbaceous wings, these basiscopically decurrent onto the axis of the next order above or below; ultimate segments lobed or crenate, the apices subentire or more commonly shallowly and obtusely dentate; veins distinct, sometimes prominulous adaxially, the sterile tips slender to slightly thickened, terminating short of the margin; sori commonly borne in the sinus between lobes of acroscopic segments or, less often, on a smaller lobe above the sinus; indusium commonly globose, about as long as broad.

This might be confused with *D. bipinnata*, under which see further discussion.

DICTYOXIPHIMUM W. J. Hooker

Plants of medium size, terrestrial, erect; rhizome erect or suberect, provided with dark-brown, lanceolate to ovate scales; leaves caespitose, sessile or subsessile, subdimorphous, the fertile ones to 85 cm. long and 6.5 cm. broad, sterile ones to 60 cm. long and 3.5 cm. broad; petiole lacking or very short, dark-scaly, not articulate at the rhizome; lamina lanceolate or oblanceolate, attenuate at base and apex, firm-herbaceous to subcoriaceous, the margin entire, usually revolute, glabrous except for a few scales along the abaxial side of the rachis; veins copiously anastomosing, the areoles with free included veinlets spreading in all directions; sorus continuous along each margin of the fertile lamina; indusium and receptacle continuous, borne along the abaxial edge of the lamina very near the thickened margin, an adaxial indusium lacking; the long-stalked sporangia mostly marginal, densely crowded, with many extending over to the adaxial edge of the lamina; spores brown, oblong-ovoid, with perine sharply and deeply folded.

This is a monotypic genus of lowland forests, confined chiefly to Central America. Affinities are with *Tectaria* and *Pleuroderris* (for further comparison, see discussion of the latter). A unique feature of the fern is the uninterrupted sorus along each margin of the fertile lamina. The sporangia are so thickly massed that they may spread over the margin, so that usually a portion of the soral line may even be observed from the adaxial side.

Dictyoxiphium panamense Hook. in Hook. and Bauer, Gen. Fil. *t.* 62. 1840. *Lindsaea panamensis* (Hook.) Mett. Fil. Hort. Bot. Lips. 105. 1856.

In wet, lowland forests, along rivers, or in ravines, 35-350 m.; Alta Verapaz; Izabal; Petén. Mexico (Chiapas); British Honduras; Honduras; Nicaragua; Costa Rica; Panama; Colombia.

Characters are those of the genus.

DIDYMOCHLAENA Desvaux

Large, terrestrial plants of wet forests; rhizome stout, erect or suberect, densely covered with linear to lanceolate, light-brown, reddish brown, or orange scales; leaves several, fasciculate, monomorphous, to about 2 m. long; petiole stout, light brown or stramineous, often subquadrangular (especially toward the base), sparsely to abundantly scaly, not articulate; lamina firm-herbaceous to chartaceous, ovate, 2-pinnate, the axes provided with linear scales and lax, tortuous trichomes; pinnae numerous, oblong, mostly ascending, sessile or subsessile, the costae and costules adaxially provided with short, antrorse awns; pinnules numerous, crowded, subsessile, somewhat articulate at the costa, submidiate, obtuse, glabrescent, subentire to crenulate, with slightly cartilaginous margins; veins free, forked, enlarged at their tips; sori elongated, abaxial on the pinnules, borne at vein tips, somewhat impressed in the tissue (thus the pinnules appearing slightly embossed adaxially); indusium elliptic, attached for most of its length along the vein; sporangia with long, slender stalks; spores monolete, broadly oblong to subspherical, with perine, irregularly tuberculate.



FIG. 24. *Dictyoxiphium panamense*. a, habit, $\times \frac{1}{2}$; b, portion of lamina, showing venation, $\times 2$; c, cross-section of leaf, $\times 2\frac{1}{2}$.

The genus is monotypic. A few species were proposed earlier, based on Old World material, but the characters are hardly significant or constant enough to merit such distinction. *Didymochlaena* should not be confused with any other genus. The subfalcate, subdimidiate pinnales resemble the ultimate segments of *Lindsaea* and *Adiantum*, but sori of these genera are marginal, whereas sori of *Didymochlaena* are oblique or roughly perpendicular to the margin, along the veins.

Didymochlaena truncatula (Sw.) J. Sm. J. Bot. (London) 4: 196. 1841. *Aspidium truncatulum* Sw. J. Bot. (Schrader) 1800 (2): 36. 1801. *Didymochlaena sinuosa* Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 303. 1811. *D. lunulata* Desv. Prodr. 282. 1827.

In wet forests, on slopes, and in ravines, 300-1,400 m.; Alta Verapaz; Baja Verapaz; Chiquimula; Huehuetenango; Izabal; Petén; Quezaltenango. Greater Antilles; Trinidad; southern Mexico to Panama; Colombia to the Guianas; southward to Brazil, Bolivia, and Paraguay; Old World tropics.

Characters are those of the genus.

DIPLAZIUM Swartz

REFERENCES: W. A. Sledge, The athyroid ferns of Ceylon, Bull. Brit. Mus. (Nat. Hist.) Bot. 2 (11): 275-323. 1962. A. R. Smith, *Diplazium delitescens* and the neotropical species of *Asplenium* sect. *Hymenasplenium*, Amer. Fern J. 66: 116-120. 1976.

Plants terrestrial; rhizome erect or suberect, rarely short-creeping, on larger species sometimes becoming a stout, epigenous caudex, sparsely to abundantly scaly, the scales not or scarcely clathrate, with margins entire or toothed; leaves monomorphic, commonly long-petiolate, of moderate to large size (commonly 0.8-3 m. long), petiole not articulate, glabrous or scaly (especially at base), nonalate, terete abaxially, variously sulcate adaxially; lamina simple to 3-pinnate-pinnatifid, essentially glabrous (except a few species minutely puberulent abaxially), on some species bearing a proliferous bud distally on the rachis; rachis glabrous or puberulent, often sparsely scaly; pinnae sub-equilateral or (more commonly) inequilateral at base; venation sometimes areolate, but in ours free; sori elliptic to (more commonly) linear, borne along the acroscopic side of veins and, at least some, along the basiscopic side (thus paired, back-to-back); indusium narrow, often delicate and hyaline, attached along the vein, commonly persistent, sometimes shriveling at maturity, rarely fugacious; paraphyses lacking; sporangium glabrous, the stalk relatively stout, composed of 2-3 rows of cells; spores monolete, bilateral, the perine, when present commonly loosely folded, without sharp ridges.

Diplazium is a large, pantropical genus, numbering between 300 and 400 species. Only a little floristic work has been done, and monographic studies have been sadly lacking, so circumscription of many of its species is currently in a nebulous state. While features such as

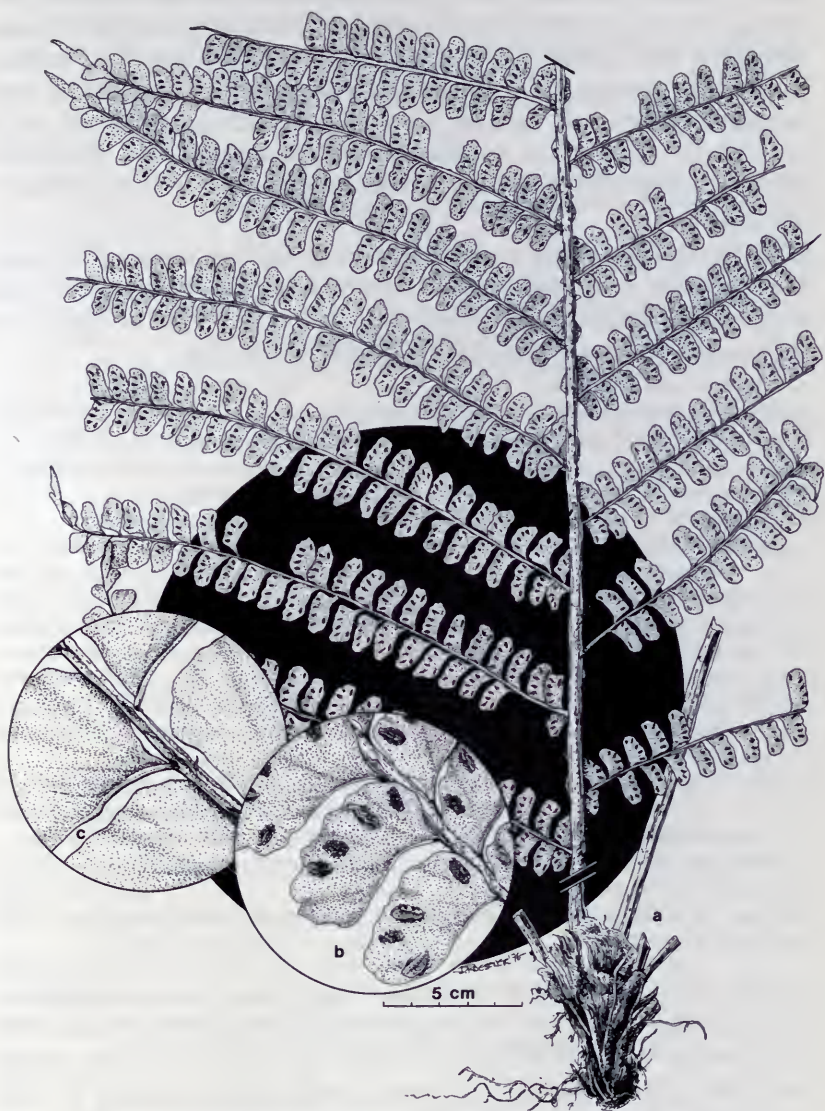


FIG. 25. *Didymochlaena truncatula*. a, habit, $\times \frac{1}{2}$; b, pinnules with sori, $\times 5$; c, portion of axis, adaxial side, with awns, $\times 10$.

scales, indusia, and leaf apices may be clearly diagnostic, many so-called species have been traditionally separated on the degree of dissection of parts, and in many cases this may be a character of extreme variability and therefore its validity may be highly suspect. Furthermore, some species may have a much wider range of distribution than is currently believed, so that they may eventually be found to be synonymous with others in different geographic locations. For these reasons, I would tend to favor a more conservative total of species in the genus.

There has also been some confusion in distinguishing *Diplazium* from the closely related genera of *Athyrium* and *Asplenium*, and some authors still prefer to combine two, or even all three, of them. See treatments of these other two for further discussion.

- a. Leaves simple or ternate.
 - b. Leaves simple; rachis lacking a proliferous bud. *D. plantaginifolium*.
 - b. Leaves ternate; rachis frequently bearing a proliferous bud at the pinna axil. *D. ternatum*.
- a. Leaves pinnate (with 2 or more pairs of pinnae) to decomound.
 - c. Pinnae entire to crenate or shallowly lobed, subequilateral at base.
 - d. Lamina pinnatifid for at least half its length; free pinnae 2-7 pairs, these to 7 (-9) cm. long. *D. verapax*.
 - d. Lamina pinnatifid (if at all) only in the apical section; free pinnae 8 to many pairs.
 - e. Lamina abruptly terminating in a subconform apical segment (this sometimes with a basal lobe); mature sori commonly 1 (rarely 2-3) to a vein, this borne on the basal acroscopic branch of the vein. *D. obscurum*.
 - e. Lamina gradually or abruptly tapering to a nonconform, pinnatifid apex; mature sori 2-6 to a vein, several of them borne on basisopic as well as acroscopic vein branches.
 - f. Veins pinnate, with 3-4 pairs of branches, the tips of adjacent branches converging (or sometimes actually merging) at the pinna margin, the tips irregularly spaced; sori commonly 2-6 to a vein, nearly equal in length.
 - g. Petiole base lacking scales; veins beneath stramineous and strongly prominulous. *D. prominulum*.
 - g. Petiole base scaly; veins beneath light or dark brown, flush or only slightly prominulous.
 - h. Larger pinnae (16) 18-32 cm. long and 3.5-5 cm. broad; lamina subcoriaceous; sori (larger ones) 8-14 mm. long. *D. neglectum*.
 - h. Larger pinnae 12-16 cm. long and 2.5-3.5 cm. broad; lamina commonly firm-membranaceous; sori (larger ones) 3-7 mm. long. *D. urticifolium*.
 - f. Veins merely 2- to 3-forked, these and their branches running in parallel fashion to the margin, their tips thus subequidistant; sori commonly 2 to a vein (a long one on the basal acroscopic branch, and a much shorter one on another branch). *D. grandifolium*.
- c. Pinnae deeply pinnatifid to bipinnate, or if subentire to shallowly lobed then inequilateral at base (cuneate or excavate basisopically, truncate and strongly produced and often auriculate acroscopically).

- i. Pinnae (or pinnules) commonly truncate and subequilateral at base, or sometimes more strongly produced basiscopically.
- j. Lamina pinnate-pinnatifid to (rarely) nearly 2-pinnate.
 - k. Indusia persistent or subpersistent; costae puberulent abaxially (especially near the base); leaf texture firm-membranaceous. *D. striatum*.
 - k. Indusia vestigial or lacking; costae essentially glabrous; leaf texture often chartaceous to subcoriaceous. *D. lindbergii*.
- j. Lamina 2-pinnate to nearly 3-pinnate.
 - l. Costules, veins, and tissue between the veins minutely (often densely) puberulent on abaxial side of lamina; texture firm-membranaceous; most veins simple. *D. expansum*.
 - l. Costules sparsely scaly, but lamina otherwise glabrous abaxially; texture commonly chartaceous; most veins 1- to 2-forked. *D. diplazioides*.
- i. Pinnae (or pinnules) inequilateral at base, cuneate to excavate basiscopically, truncate and more strongly produced acroscopically.
- m. Pinnae subentire to deeply pinnatisect, or a few basal segments free or nearly so (but never stalked).
 - n. Scales essentially lacking at base of petiole, sparse or lacking on rhizome; bases of at least some proximal pinnae subequilateral. . . *D. prominulum*.
 - n. Scales present at base of petiole, ample to abundant on rhizome apex; bases of all pinnae inequilateral.
 - o. Pinnae serrate to crenate, or shallowly lobed and then the lobes incised $\frac{1}{4}$ or less to the costa. *D. werckleanum*.
 - o. Pinnae (most of them) lobed halfway or more to the costa.
 - p. Larger pinnae lobed $\frac{1}{2}$ - $\frac{3}{4}$ to costa; basal segments never free; free portion of larger ultimate segments commonly straight, obtuse, and 1 or 2 times as long as broad. *D. cristatum*.
 - p. Larger pinnae (at least toward the base) commonly incised more than $\frac{3}{4}$ to the costa; basal acroscopic segments on larger pinnae often free or nearly so; free portion of larger ultimate segments commonly subfalcate, acute, and 2-4 times as long as broad. *D. lonchophyllum*.
- m. Pinnae pinnate to 2-pinnate-pinnatifid, at least the proximal pinnules of basal pinnae free and short-stalked.
 - q. Secondary segments subentire to pinnatisect, most of them decurrent, but usually several proximal ones of larger pinnae free and short-stalked. . . . *D. franconis*.
 - q. Secondary segments pinnatisect to pinnate-pinnatifid, most of them free (becoming decurrent toward pinna apex). *D. donnell-smithii*.

Diplazium cristatum (Desr.) Alston, J. Bot. 74: 173. 1936. *Meniscium cristatum* Desr. in Lam. Encycl. 4: 94. 1797. *Asplenium arboreum* Willd. in L. Sp. Pl. 5: 320. 1810. *A. denticulosum* Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 323. 1811 (not Gaud. 1827). *A. shepherdii* Spreng. Nova Acta Phys.-Med. Acad. 10: 231, t. 17, f. 5-6. 1821. *D. shepherdii* (Spreng.) Link, Hort. Reg. Bot. Berol. 2: 70. 1833. *D. arboreum* (Willd.) Presl, Tent. Pterid. 114. 1836. *D. denticulosum* (Desv.) C. Chr. Index Fil. 231. 1905.

In wet forests, thickets, and wooded ravines, 800-1,550 m.; Alta

Verapaz; Baja Verapaz; Escuintla; Santa Rosa. West Indies; Mexico to Colombia and Venezuela, southward to Argentina and Paraguay.

Plants terrestrial; rhizome erect, provided at apex with ovate to lanceolate scales, these dark brown to blackish, often lustrous, 2-4 mm. long; leaves crowded to fasciculate, 25-80 cm. long, 8-25 cm. broad; petiole 8-40 cm. long, equaling or shorter than the lamina, yellowish to gray- or red-brown, subterete abaxially, sulcate adaxially, scaly near the base (the scales 2-4 mm. long, dark brown), otherwise glabrous; lamina pinnate-pinnatifid, ovate to lanceolate, firm-membranaceous, essentially glabrous, gradually terminating in a pinnatifid apex; rachis yellow- to gray-brown, glabrous, lacking a proliferous bud; pinnae 8-12 free pairs, proximal ones short-stalked, distal ones adnate, 6-13 cm. long, 1-3 cm. broad, deltoid-lanceolate, mostly subfalcate, attenuate at apex, inequilateral at base (narrowly cuneate to excavate basiscopically, truncate and strongly produced acroscopically), most of them pinnatifid, larger ones cut $\frac{1}{2}$ - $\frac{3}{4}$ to the costa; costa glabrous, stramineous to gray-brown, slightly to strongly prominulous abaxially, adaxially flush or immersed and often flanked by raised, parallel, cartilaginous ribs; ultimate segments 10-12 pairs, commonly straight and obtuse (rarely acute) and spreading from the costa at a broad angle, the free portion 1-2 times as long as broad; veins distinct (at least abaxially), pinnately branched in the segments, flush with the leaf surface or (rarely) slightly prominulous; sori 1-4 (-6) in each segment, that of the basal acroscopic vein branch longer and curved, the others commonly shorter and straight, usually only the basal one double; indusium linear, ample, dark brown, persistent.

With this perhaps might be included *D. werckleanum* and *D. lonchophyllum* (also *D. franconis?*), along with numerous other taxa which have already been placed in synonymy under one of these names by modern workers. The three have been traditionally separated by the degree of dissection of pinnae or the relative length of basal segments (and little else). Rather simply stated, for purposes of this treatment I have provisionally maintained *D. werckleanum* (pinnae lobed $\frac{1}{3}$ or less to the costa), *D. lonchophyllum* (pinnae cut $\frac{3}{4}$ or more to the costa), and *D. cristatum* (everything in between). Based upon all the material I have seen from Central and South America and the West Indies, the line of demarcation between each "species" is rather faint. For example, Alston (1936, *loc. cit.*) placed *D. arboreum* with *D. cristatum* and, judging from the types of both, it would appear that the former is perfectly intermediate between *D. cristatum* and *D. werckleanum*. Thus it would probably be more realistic to consider them all at an infraspecific level, but such a decision must come as a result of more careful field and greenhouse observations, and a comparison of mass collections throughout the entire range of distribution.

Diplazium diplazioides (Kl. & Karst.) Alston, J. Bot. 74: 174. 1936. *Lotzea diplazioides* Kl. & Karst. Linnaea 20: 358. 1847. *Asplenium klotzschii* Mett. Fil. Hort. Lips. 79. 1856. *D. klotzschii* (Mett.) Moore, Index Fil. LV. 1857.

In dense, wet forests, 1,400-2,400 m.; Alta Verapaz; San Marcos.

Southern Mexico; Honduras; Nicaragua; Costa Rica; Lesser Antilles; Trinidad; Colombia; Venezuela.

Plants terrestrial, rhizome not seen (but plants sometimes described on herbarium labels as "arborescent"); leaves to 3 m. long and 1 m. broad; petiole 0.6-1 m. long, stramineous to light brown, subterete abaxially, sulcate adaxially, scaly near the base (the scales to 2.5 cm. long, dark brown, linear to lanceolate), otherwise glabrous; lamina 2-pinnate-pinnatifid, or nearly 3-pinnate as to the bases of larger pinnae, commonly chartaceous, essentially glabrous, gradually terminating in a pinnatifid apex; rachis stramineous, glabrous, but sparsely provided with dark-brown, linear to filamentous scales, lacking a proliferous bud; pinnae numerous, stalked, larger ones 20-50 cm. long, 15-25 cm. broad, ovate to lanceolate, acuminate at apex, truncate and subequilateral at base; costa stramineous (to light brown adaxially), sparsely to amply provided with linear to filamentous, light- or dark-brown scales, adaxially often minutely puberulent; pinnules 12-18 pairs on larger pinnae, mostly short-stalked, deeply incised (basal ones often nearly to the costule), acute to acuminate at apex, truncate and subequilateral at base (or the basal basiscopic segment somewhat larger than the acroscopic one); costules sparsely to amply provided abaxially with amber to dark-brown, ovate to linear, attenuate scales, adaxially minutely puberulent between the raised, parallel wings of tissue; ultimate segments 10-14 pairs, surfaces glabrous, rounded to truncate (rarely acute) at the apex, the margins entire, serrate or (rarely) crenate-serrate, often somewhat revolute; veins distinct (at least abaxially), pinnately branched, the branches 1- to 2-forked or (less commonly) simple; sori relatively short, 1-2.5 mm. long, extending from midvein one-third to halfway to the margin, most of them single, usually only the basal ones double; indusium linear to elliptic, dark brown, erose to ciliate-erose, subsistent.

This is similar to *D. expansum*, under which see further comparison.

Diplazium donnell-smithii Christ, Bull. Herb. Boissier II. 7. 270. 1907 (type from San Pedro Sula, Dept. Santa Barbara, Honduras, *Thieme 5680*).

In wet forests or thickets, 1,300-1,600 m.; Alta Verapaz; Chimaltenango. Honduras; El Salvador; Nicaragua; Costa Rica.

Plants terrestrial; rhizome erect, relatively slender, amply provided with lanceolate, brown scales, these to 1 cm. long and 0.15 cm. broad; leaves to 1.5 m. long and 0.5 m. broad, crowded to fasciculate; petiole stramineous to yellow- or gray-brown, equaling or nearly equaling the lamina, subterete abaxially, sulcate adaxially, scaly at base, the scales 5-8 mm. long, dark brown, lanceolate; lamina 2-pinnate-pinnatisect to 3-pinnate, chartaceous, gradually terminating in a pinnatifid apex; rachis stramineous to yellowish brown, essentially glabrous, but sometimes provided with a few, scattered, dark-brown, filamentous scales, lacking a proliferous bud; pinnae stalked, larger ones 17-34 cm. long, 6-16 cm. broad, ovate to lanceolate, acute to acuminate at apex, subequilateral to (more commonly) inequilateral at base (more strongly produced acroscopically); costa stramineous to yellow-brown, sparsely scaly, the scales minute, dark brown, filamentous; pinnules 12-16 pairs on larger pinnae, most of them free, short-stalked, pinnatisect to pinnate-pinnatifid, acute to acuminate at apex, inequilateral at base (narrow-cuneate basiscopically, truncate and more strongly produced acroscopically); ultimate segments decurrent (or basal ones of largest pinnules free or nearly so), obliquely ascending, inequilateral at base, obtuse to subacute at apex, serrate to crenate or deeply lobed,

essentially glabrous; veins distinct to indistinct, pinnately branched, the branches simple to 1-forked; sori relatively long (2-3 mm.) and narrow, extending halfway to nearly all the way from midvein to margin, usually only the basal ones double; indusium linear, dark brown, subentire, persistent.

Diplazium expansum Willd. Sp. Pl. 5: 354. 1810. *Asplenium expansum* (Willd.) Presl, Rel. Haenk. 1: 46. 1825. *Athyrium expansum* (Willd.) Milde, Bot. Zeit. 353. 1870 (not Moore, 1860).

In dense, wet forests or wooded ravines, 1,200-2,700 m.; Alta Verapaz; San Marcos. Mexico; Greater Antilles; Colombia; Venezuela; Brazil; Ecuador; Peru.

Plants terrestrial; rhizome not seen, presumably thick and erect; leaves to 2 m. long and 0.7 m. broad; petiole 25-75 cm. long, shorter than or nearly equaling the lamina, subterete abaxially, sulcate adaxially, scaly near the base (the scales to 2 cm. long, dark brown, linear to lanceolate) and often minutely puberulent; lamina 2-pinnate-pinnatifid, ovate, firm-membranaceous, minutely puberulent on axes, veins, and leaf surface abaxially, gradually terminating in a pinnatifid apex; rachis stramineous to light brown, minutely (and often densely) puberulent, lacking a proliferous bud; pinnae numerous, stalked, larger ones 20-35 cm. long, 12-18 cm. broad, ovate to lanceolate, acuminate at apex, truncate and subequilateral at base; costa stramineous, puberulent and sparsely brown-scaly; pinnules 12-15 pairs on larger pinnae, mostly short-stalked, deeply incised (basal ones often nearly to the costule), acute to acuminate at the apex, truncate and subequilateral at base (or the basal basiscopic segment somewhat larger than the basal acroscopic one); costules puberulent and sparsely provided with dark-brown, linear, attenuate scales; ultimate segments 8-12 pairs, minutely puberulent abaxially on and between the veins, rounded to truncate (rarely acute) at the apex, the margins entire to serrate; veins distinct (at least abaxially), pinnately branched, the branches simple or (less commonly) 1-forked near the margin; sori commonly short (only rarely extending to near the margin), most of them single, usually only the basal ones double; indusium linear, thin, dark brown, often ciliate-erose, subpersistent.

This and *D. diplazioides* are very similar, scarcely differing other than in those features noted in the key. I am not certain that I have properly applied the names to these two species, for they are a part of a rather large and confusing complex, including at least a dozen species (or names) in the neotropics. A complete study of all the types and literature is necessary before the taxonomy and nomenclature may be settled. A few of the names involved are: *Asplenium radicans* Schkuhr, 1809 *p. p.*; *A. dubium* Mett. 1859; *D. ambiguum* Raddi, 1819; *D. amplum* Liebm. 1849. Most of the supposed differences in these species involve texture, degree of dissection and pubescence, and margins of segments and indusia—all of which could be merely the products of size and maturity of the leaf.

Diplazium franconis Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 256 (seors. 104). 1849. *Asplenium shepherdii*

Spreng. var. *bipinnatum* Christ, Bot. Gaz. 20: 545. 1895 (type from Volcan Tecuamburro, Santa Rosa, Heyde & Lux 4680).

Common, in wet forests, thickets, or deeply shaded ravines, 100-2,800 m.; Alta Verapaz; Chimaltenango; Izabal; Petén; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Suchitepéquez. Southern Mexico (type from Villa Alta, Oaxaca, Liebmann 790); British Honduras; El Salvador; Nicaragua; Costa Rica.

Plants terrestrial; rhizome erect, on larger plants sometimes becoming a stout, epigenous caudex to 30 cm. long and 3 cm. thick, sparsely to amply provided at apex with light- to dark-brown, linear to narrow-ovate scales; leaves crowded to fasciculate, highly variable in size, mature ones 0.5-1 (1.5) m. long, 0.2-0.4 (0.6) m. broad; petiole yellowish to brown, 20-50 (70) cm. long, shorter than the lamina, sparsely to amply scaly toward or at the base, the scales 5-15 mm. long, 0.1-5.0 mm. broad, filiform to narrow-ovate, often deciduous; lamina 2-pinnate to 2-pinnate-pinnatifid, chartaceous, gradually terminating in a pinnatifid apex; rachis stramineous to light brown, glabrous, lacking a proliferous bud; pinnae stalked, larger ones 10-30 (-38) cm. long, 3.5-10 (-20) cm. broad, ovate to lanceolate, acute to attenuate at apex, subequilateral to (more commonly) inequilateral at base (more strongly produced acroscopically); costa stramineous, sparsely provided with linear to filamentous dark-brown scales, these often deciduous; pinnules (secondary segments) 12-22 pairs on larger pinnae, subentire to pinnatisect, mostly decurrent, but often several proximal ones of larger pinnae free and short-stalked, obtuse to acute at apex, inequilateral at base (narrow-cuneate or excavate basiscopically, truncate and more strongly produced acroscopically); veins distinct to indistinct, pinnately branched in the ultimate segments, the branches simple or forked; sori relatively long (3-6 mm.) and narrow, extending halfway to nearly all the way from midrib to margin, usually only the basal ones double; indusium linear, yellowish to dark brown, subentire, persistent.

This may be merely a luxuriant, more highly divided variant of *D. lonchophyllum*, and thus but another component of the *D. cristatum* complex. (See discussion under the latter species for further elaboration.) Of all the species in the genus, *D. franconis* exhibits perhaps the greatest variability in leaf size. Indeed, it might be tempting to split it into several varieties, were it not for the fact that the taxonomic status of the species itself is so uncertain at this time. In Guatemala, the most typical leaf ranges from 75-110 cm. in length and 27-40 cm. in breadth, with larger pinnae about 15-30 cm. long and 5-10 cm. broad. However, at least two collections (*Steyemark 33409 & 33875* from Quezaltenango) have exceedingly large leaves, 140-160 cm. long and 55-60 cm. broad, with pinnae 32-38 cm. long and 17-20 cm. broad. Yet in all other respects these specimens differ scarcely from the typical.

There is another, larger group of specimens (1,200-2,400 m., Chimaltenango; Quezaltenango; Sololá) which differ more substantially. Leaf and pinna size are consistently smaller than the typical, pinnae and ultimate segments are less crowded, much narrower, and

usually more acute. Even more significantly, the rhizome scales are linear to filiform, 0.1-0.8 mm. broad, and rather abundant, whereas rhizome scales in typical *D. franconis* are commonly lanceolate to lance-ovate and 2-3 (5) mm. broad, and not particularly numerous. These specimens superficially resemble a photograph of the holotype (Galeotti 6483, Paris) of *Asplenium aspidiiforme* Fée (Gen. Fil. 199. 1852), a supposed synonym of *D. franconis*, and may merit at least infraspecific status. The question deserves future consideration.

Diplazium grandifolium (Sw.) Sw. J. Bot. (Schrader) 1800 (2): 62. 1801. *Asplenium grandifolium* Sw. Prodr. Veg. Ind. Occ. 130. 1788.

In lowland rain forests, sea level to 500 m.; Izabal; Petén. Honduras; Nicaragua; Costa Rica; Panama; Greater Antilles; Trinidad & Tobago; Venezuela; Colombia; Ecuador; Peru.

Plants terrestrial; rhizome erect, provided at apex with dull, dark-brown or blackish scales, these linear or linear-lanceolate, 2-7 mm. long; leaves crowded to fasciculate, mature ones 50-120 cm. long and 17-28 cm. broad; petiole shorter than the lamina, dull reddish or grayish brown, subquadrangular, sulcate adaxially, near the base provided with dark-brown to blackish scales, these mostly linear, to 0.8 cm. long, entire to irregularly and minutely denticulate; lamina pinnate, ovate, firm-herbaceous to chartaceous, glabrous, gradually terminating in a pinnatifid apex; rachis yellowish to reddish brown, essentially glabrous but sometimes sparsely provided with minute, unicellular trichomes ca. 0.1 mm. long, lacking a proliferous bud; pinnae 8-12 free pairs, lower and middle ones short-stalked, larger ones (9) 10-14 cm. long, 2-3.5 cm. broad, acuminate at apex, broadly cuneate to truncate at base, the margin entire to broadly crenulate; costae scarcely prominulous abaxially, commonly flattened adaxially, but usually flanked by 2 slightly raised, parallel ridges of tissue, and amply provided with minute, yellowish or brownish, unicellular trichomes between the ridges; veins commonly distinct (at least abaxially), these and 2 or 3 branches running in subparallel fashion to the pinna margin, their tips essentially equidistant; sori elongated in usually 2 (sometimes 3) series on each side of the costa, a long one running nearly the length of the basal acroscopic branch, and 1 (or 2) much shorter ones borne on other branches; indusia narrow, delicate, and scarious or yellowish, ca. 0.5 mm. broad, but becoming constricted and dark brown at maturity.

Diplazium lindbergii (Mett.) Christ, Prim. Fl. Costaric. 3: 27. 1901. *Asplenium lindbergii* Mett. Ann. Sci. Nat. Bot. V, 2: 236. 1864. *A. induratum* Christ, Bull. Soc. Roy. Bot. Belgique 35: Mem. 201. 1896 nom. illeg. (not *A. induratum* Hook. 1861). *D. induratum* Diels in Engl. & Prantl, Nat. Pflanz. 1(4): 226. 1899.

In wet forests, thickets, or wooded ravines, 1,150-2,300 m.; Alta Verapaz; Baja Verapaz; Quezaltenango; San Marcos; Zacapa. Southern Mexico; Honduras to Panama; Colombia to Brazil and Bolivia.

Plants terrestrial; rhizome not seen, presumably erect; leaves reportedly caespitose, to 1.5 m. long and 0.45 m. broad; petiole to 80 cm. long, shorter than the lamina,



FIG. 26. *Diplazium*. a, *D. striatum*, habit, $\times \frac{1}{2}$; b, *D. obscurum*, leaf apex, $\times \frac{1}{2}$; c, *D. werckleanum*, pinna, $\times \frac{1}{2}$; d, *D. grandifolium*, portion of pinna with sori, $\times 3$.

subterete abaxially, commonly sulcate adaxially, dark or reddish brown, subglabrous distally, but amply scaly near the base, the scales to 1.5 cm. long, dark brown, linear to lanceolate, with the cells mostly 3-4 times as long as broad; lamina pinnate-pinnatifid, ovate or deltoid-ovate, chartaceous to subcoriaceous, essentially glabrous (or costa and veins sparsely provided with minute scales), gradually terminating in a pinnatifid apex; rachis dull yellowish to reddish brown, essentially glabrous, lacking a proliferous bud; pinnae 12-20 pairs, most of them short-stalked, larger ones 18-26 (-30) cm. long, 3.5-4.5 (-6) cm. broad, lanceolate or linear-lanceolate, acuminate or attenuate at apex, truncate and subequilateral at base, deeply pinnatifid, cut $\frac{3}{4}$ - $\frac{7}{8}$ to the costa; costa glabrous or subglabrous, commonly prominulous and 3-ridged abaxially, essentially plane adaxially, but provided with parallel wings of tissue perpendicular to the surface, these awned at the bases of the costules; ultimate segments more than 20 pairs on larger pinnae, subfalcate, obtuse (or rarely acute), spreading at a broad (ca. 90°) angle from the costa, margin subentire to serrulate, often strongly revolute, the basal basiscopic one commonly larger than the basal acroscopic one; veins distinct (at least abaxially), simple to 1-forked; sori inframedial, borne near the costule and extending $\frac{1}{3}$ - $\frac{1}{2}$ (- $\frac{3}{4}$) of the way to the margin, on forked veins commonly borne below the fork, or extending slightly onto the acroscopic branch; indusium vestigial or lacking.

With this probably should be included *D. grande* (Bak.) C. Chr. from northern South America. I have not seen the type, but judging from specimens so determined and from the original description (under *Gymnogramme grandis* Bak. in Hook. & Bak. Syn. Fil. 377. 1868) there seem to be no significant differences.

Diplazium lonchophyllum Kze. Linnaea 13: 141. 1839 (not 1848). *D. inaequilaterum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 255 (seors. 103). 1849. *Asplenium inaequilaterale* (Liebm) Fée, Mém. Fam. Foug. 9: 17. 1857 (not Willd. 1810, nor Mart. & Gal. 1842). *A. lonchophyllum* (Kze.) Mett. Abh. Senckenberg Naturf. Ges. VI: *Asplen.* 205. 1859. *A. inaequilaterum* (Liebm.) Mett. *tom. cit.* 210.

In wet forests, thickets, and wooded ravines, 200-2,500 m.; Alta Verapaz; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Quezaltenango; Retalhuleu; Sacatepéquez; Santa Rosa. Mexico to Panama.

Plants terrestrial; rhizome erect, provided at apex with ovate to lanceolate scales, these dark brown to blackish, sometimes lustrous, 2-4 mm. long; leaves fasciculate, 32-80 cm. long, 8-22 cm. broad; petiole 7-38 cm. long, shorter than the lamina, yellowish to grayish brown, subterete abaxially, sulcate adaxially, scaly near the base (the scales 2-4 mm. long, light or dark brown), otherwise glabrous; lamina pinnate-pinnatifid, ovate to lanceolate, firm-membranaceous, essentially glabrous, gradually terminating in a pinnatifid apex; rachis yellowish to grayish brown, glabrous, lacking a proliferous bud; pinnae 10-18 free pairs, most of them short-stalked, 6-18 cm. long, 1.5-4.5 cm. broad, deltoid-lanceolate, mostly subfalcate, attenuate at apex, inequilateral at base (narrowly cuneate to excavate basiscopically, truncate and strongly produced acroscopically), most of them deeply pinnatifid, larger ones cut $\frac{3}{4}$ or quite to the costa; costa glabrous, stramineous to gray-brown, slightly to strongly prominulous abaxially, adaxially flush or

immersed, and often flanked by raised, parallel ribs or wings of tissue; ultimate segments 10-17 pairs, commonly subfalcate and acute and spreading obliquely from the costa, the free portion 2-4 times as long as broad; veins distinct (at least abaxially), pinnately branched in the segments, flush with the leaf surface or slightly prominulous, sori 1-4 (-6) in each segment, that of the basal acroscopic vein branch usually longer and curved, the others shorter and straight, usually only the basal one double; indusium linear, ample, dark brown, persistent.

This might perhaps be better considered only a variety of *D. cristatum*, under which see further discussion.

***Diplazium neglectum* (Karst.) C. Chr. Index Fil. 236. 1905.**
Asplenium neglectum Karst. Fl. Columb. 1: 106, t. 52. 1860.

In wet, montane forests, 1,800-2,400 m.; Quezaltenango; San Marcos. Southern Mexico (Chiapas); Costa Rica; Panama; Colombia.

Plants terrestrial; rhizome erect, scaly at the apex, leaves fasciculate, to 1.5 m. long and 0.5 m. broad; petiole dark reddish brown, subquadrangular, sulcate adaxially, amply to sparsely provided with dull-brown scales, these linear to lanceolate, 1-2 cm. long, 0.1-0.3 cm. broad; lamina pinnate, ovate to broadly lanceolate, subcoriaceous, essentially glabrous, abruptly terminating in a nonconform, pinnatifid apical section, this deeply lobed at base; rachis dark reddish brown, sparsely to amply provided with tortuous, linear, often filiform scales, sulcate adaxially, commonly bearing a proliferous bud in the axil of one or more of the distal pinnae; pinnae 8-16 pairs, most of them stalked, larger ones (16) 18-32 cm. long, 3.5-5 cm. broad, lanceolate or oblong-lanceolate, acute to attenuate at apex, broadly rounded to truncate at base, the margins subentire to crenate, or at base lobed nearly halfway to the costa; costa dark reddish or grayish brown, prominulous and sparsely provided with dull-brown, linear scales abaxially, flattened or slightly immersed adaxially and flanked by 2 inconspicuous parallel ridges; veins distinct, light to dark brown, abaxially flush or slightly prominulous, pinnately branched, the branches 3-4 pairs, with tips of lower ones often tending to converge with tips of adjacent branches at the pinna margin; sori subequal, commonly in 3-5 series on each side of the costa, elongated, larger ones 8-14 mm. long, borne nearer the midvein than the margin; indusia dull brown, rather narrow, persistent, those of the proximal 1-2 vein branches usually double.

***Diplazium obscurum* Christ, Bull. Herb. Boissier II. 7: 269. 1907.**
D. flavescens (Mett.) Christ var. *proliferum* Christ, op. cit. 5: 729. 1905.

Apparently represented in Guatemala by a single collection: terrestrial, Montaña Canahui, El Progreso, alt. 1,600-2,300 m. (*Steyermark 43790*). Honduras; Nicaragua; Costa Rica; Panama.

Plants terrestrial; rhizome erect, sparsely scaly at apex; leaves crowded to fasciculate, to 1.5 m. long and 0.4 m. broad; petiole dark reddish or grayish brown, subquadrangular, sulcate adaxially, provided near the base with dull-brown scales, these lanceolate to ovate, to 1 cm. long and 0.3 cm. broad, entire or irregularly and minutely denticulate; lamina pinnate, ovate, chartaceous, glabrous, abruptly terminating in a subconform apical segment, this resembling the middle pinnae, but often with an enlarged, basal lobe; rachis dark reddish brown, glabrous, or with a few scattered, linear, dark scales,

sulcate adaxially, commonly bearing a proliferous bud in the axil of 1 or more of the distal pinnae; pinnae 8-12 pairs, lower and middle ones short-stalked, 15-25 cm. long and 3-4.5 cm. broad, acuminate at apex, narrowly to broadly rounded or subtruncate at base, the margins entire or broadly serrate; costa prominulous abaxially, commonly flattened adaxially, but often flanked by 2 inconspicuous parallel wings of tissue perpendicular to the surface, glabrous adaxially, sparsely provided on abaxial side with minute, linear or hairlike scales; veins commonly distinct, these and 2-4 branches running in parallel fashion to the pinna margin; sori commonly in a single series on each side of the costa and borne on the basal acroscopic vein branch (or rarely in 2-3 series and a few borne on the basiscopic branches), elongated, to 1.5 cm. long, borne nearer the costa than the margin; indusia dull brown, very narrow, and usually only partly covering the sporangia (often shriveling and inconspicuous at maturity), most of them double.

Diplazium flavescens var. *proliferum* is identical with *D. obscurum*. However, typical *D. flavescens*, a fern of South America and the Greater Antilles, though superficially similar, may be distinguished from our plant by the following features: the texture is thinner (usually firm-membranaceous), the apical section of the lamina more closely matches the shape of the larger pinnae, the rachis and petiole are stramineous to light yellowish brown, and the proliferous bud is lacking on the rachis.

Diplazium plantaginifolium (L.) Urban, Symb. Antill. 4: 31. 1903. *Asplenium plantaginifolium* L. Syst. Nat. ed. 10, 2: 1323. 1759. *A. plantagineum* L. Sp. Pl. 1537. 1763. *D. plantagineum* (L.) Sw. J. Bot. (Schrader) 1800 (2): 62. 1801.

In rain forests, on slopes or ridges, 300-1,000 m.; Alta Verapaz; Izabal; San Marcos; Santa Rosa. Southern Mexico to Panama; West Indies; Venezuela; Brazil; Peru; Bolivia.

Plants terrestrial; rhizome erect or ascending, sparsely provided at the apex with inconspicuous, deep reddish brown scales, these lanceolate to ovate, 1-2 mm. long; leaves to 70 cm. long, simple, unlobed, erect, fasciculate; petiole to 40 cm. long, as long as or longer than the lamina, sparsely and minutely scaly at base, stramineous to yellow- or gray-brown; lamina 3.5-7 cm. broad, glabrous, lanceolate to oblong-lanceolate, acuminate at the apex, broadly cuneate to truncate at base, the margins subentire proximally to serrate or crenate-serrate distally; costa yellowish, strongly raised abaxially, adaxially sulcate, slightly depressed (or appearing so because of the raised marginal ridges), lacking a proliferous bud; veins distinct or indistinct, spreading at a broad angle from the costa, with 2-4 pairs of strongly ascending branches, these and the main vein running in parallel fashion out to the margin; sori often crowded, greatly elongated, some of them extending nearly from costa to margin; indusia brownish, delicate, and very narrow, many of them double.

The simple lamina of *D. plantaginifolium* distinguishes it from all other species of *Diplazium* in Guatemala. Rare specimens have been observed elsewhere which are deeply lobed at base, thus appearing similar to *D. ternatum*. But even in these cases the basal lobes are

adnate, and connected to the apical section with a wing of tissue. In *D. ternatum*, the apical section is free, and the lateral pinnae are at least short-stalked.

Diplazium prominulum Maxon, Contr. U.S. Natl. Herb. 13: 15. 1909.

Rare; in wet forests, 1,400-1,500 m.; Alta Verapaz; Baja Verapaz (type from "Wald zwischen Purulhá und Panzal," *Tuerckheim II-1683*).

Plants terrestrial, rhizome erect, rather slender, with scales lacking or few and deciduous; leaves fasciculate, 50-70 cm. long, 15-18 cm. broad; petiole 20-30 cm. long, naked, yellowish except at the dark-brown, subterete base, sulcate adaxially; lamina pinnate-pinnatifid, ovate, chartaceous, glabrous throughout, gradually terminating in a pinnatifid apex; rachis yellowish, lacking a proliferous bud, slightly flexuous toward the apex; pinnae 10-12 pairs, straight or only slightly falcate, proximal ones short-stalked, distal ones adnate, larger ones 9-10 cm. long, 2.5-3 cm. broad, lanceolate, acute at the apex, the base truncate to broadly cuneate, subequilateral (or somewhat inequilateral on some distal pinnae), margins crenate or shallowly to deeply lobed; costa glabrous, yellowish, strongly prominulous abaxially, provided with parallel cartilaginous ridges adaxially; ultimate segments (or crenations) 8-10 pairs on larger pinnae, obtuse to subacute, the basal pair smaller than or equal to the adjacent pair, separated by rather broad sinuses; veins distinct, pinnately branched in the segments, stramineous abaxially and strongly prominulous; sori 1-8 to a segment, 2-7 mm. long, commonly only those of the basal acroscopic branch double; indusium dark to light brown, persistent.

Although a number of Central American collections (outside Guatemala) seen in various herbaria have been identified as this species, none that I have seen clearly match the type. These specimens are glabrous, and lack petiole base scales, as in *D. prominulum*, but here the resemblance ends. Otherwise, they have subfalcate, long-acuminate, or attenuate pinnae with strongly inequilateral bases as in *D. cristatum* (narrowly cuneate or excavate basiscopically but truncate and strongly produced acroscopically), and the veins are flush and not particularly distinct. Pinnae in *D. prominulum* are acute or subacute, with essentially equilateral bases, and the costae, midribs, and veins are strongly prominulous.

Diplazium striatum (L.) Presl, Tent. Pterid. 114. 1836 (not Desv. 1827, nor Hook. 1838). *Asplenium striatum* L. Sp. Pl. 1082. 1753. *D. crenulatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 254 (seors. 102). 1849. *A. crenulatum* (Liebm.) Bak. in Hook. & Bak. Syn. Fil. 236. 1867. *D. striatastrum* Lell. Selbyana 2: 283. 1978.

In wet forests and wooded ravines, 500-2,400 m.; Alta Verapaz; Izabal; Quezaltenango; Retalhuleu; Sacatepéquez; Suchitepéquez;

Zacapa. West Indies; Southern Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Colombia; Venezuela; Ecuador; Peru.

Plants terrestrial; rhizome erect, rather elongated, near the apex provided with dark-brown, ovate to lanceolate scales, these to 1 cm. long, sometimes slightly lustrous; leaves crowded to fasciculate, 0.8-2 m. long, 0.15-0.5 m. broad; petiole 30-70 cm. long, shorter than the lamina, subterete abaxially, sulcate adaxially, amply scaly near the base (the scales to 1.5 cm. long, dark brown, lanceolate) and amply but minutely puberulent throughout (the trichomes mostly 0.1-0.2 mm. long, pluricellular); lamina pinnate-pinnatifid to nearly 2-pinnate (as to the bases of larger pinnae), ovate to lanceolate, firm-membranaceous, minutely puberulent (at least on the axes), gradually terminating in a pinnatifid apex; rachis stramineous to reddish brown, minutely (and often densely) puberulent, or glabrate, lacking a proliferous bud; pinnae 15-25 pairs, most of them short-stalked, larger ones 10-30 cm. long and 2-6 cm. broad, lanceolate or deltoid-lanceolate, acuminate or attenuate at apex, truncate and subequilateral at base, deeply pinnatifid, most of them cut $\frac{1}{2}$ - $\frac{3}{4}$ to the costa, or, as to the bases of larger pinnae often cut nearly or quite to the costa, thus a few pinnules free or nearly so; costa minutely puberulent, especially near the base, abaxially plane or slightly prominulous toward the base, adaxially plane, but provided with parallel wings of tissue perpendicular to the surface, these usually awned at the bases of the costules; ultimate segments 12-24 pairs, often puberulent abaxially, straight or subfalcate, obtuse (or rarely acute), spreading at a broad (ca. 90°) angle from the costa, margin essentially plane, entire to serrulate, or at the apex serrate, the basal basisopic one often larger than the basal acroscopic one; veins distinct (at least abaxially), simple to 1-forked; sori extending from the costule $\frac{3}{4}$ - $\frac{5}{8}$ of the way to the margin, on forked veins extending well out along the acroscopic branch; indusium linear, ample, brown, persistent or subpersistent.

This and *D. crenulatum* supposedly differed in the size of the pinnae and the depth of cutting of the segments, the latter name being applied to specimens with larger pinnae 5 and 6 cm. broad and cut nearly or quite to the costa. Plants with pinnae 2-3 cm. broad, cut $\frac{1}{2}$ - $\frac{3}{4}$ to costa, were determined as *D. striatum*. However, in examining large numbers of collections throughout the range of the species, one discovers that characters such as pinna size and degree of dissection merge imperceptibly. For example, I can see no point of demarcation between plants with narrower pinnae cut $\frac{3}{4}$ to the costa and those with broader pinnae cut entirely to the costa. Furthermore I have seen a number of specimens in which narrower pinnae are more highly dissected, and others in which the converse is true. Lellinger's new species, *D. striatastrum*, essentially is based on these same kinds of features, which are undistinguishable to me.

Diplazium ternatum Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 252 (seors. 100). 1849. *Asplenium ternatum* (Liebm.) Hook. Sp. Fil. 3: 265. 1860.

In rain forests, 950-1,600 m.; Alta Verapaz; Baja Verapaz. Southern Mexico (type from Oaxaca, *Liebmann 2385*); Honduras; El Salvador; Nicaragua.

Plants terrestrial; rhizome erect, sparsely provided at apex with inconspicuous, deep reddish brown ovate scales about 1 mm. long; leaves approximate to fasciculate, 25-55 cm. long, 8-15 cm. broad; petiole yellow- to olive-brown, nearly equaling or much longer than the lamina, sparsely scaly at base; lamina ternate, consisting of 1 pair of pinnae and a conform, but slightly larger, free apical segment, glabrous, firm-herbaceous to chartaceous; rachis frequently bearing a proliferous bud at the pinna axil; pinnae short-stalked, ovate to lanceolate, often subfalcate, acute to acuminate, cuneate to subtruncate at base, the margins serrate or crenate-serrate, the costa yellowish and prominulous abaxially, shallow-sulcate adaxially; veins distinct to (adaxially) obscure, pinnately branched, the branches and main vein running in parallel fashion out to the margin, an occasional branch reconverging to form a narrow areole; sori often crowded, elongated (sometimes greatly so), some of them frequently extending $\frac{3}{4}$ the distance between costa and margin; indusia scarious, yellowish or light brown, delicate, to 0.7 mm. broad, but commonly more constricted at maturity, many of them double.

***Diplazium urticifolium* Christ, Prim. Fl. Costaric. 3: 29. 1901.**

In wet forests or in wooded ravines, 1,200-1,600 m.; Alta Verapaz; Baja Verapaz; Quezaltenango. British Honduras; Honduras; Nicaragua; Costa Rica.

Plants terrestrial; rhizome erect, provided at apex with brown, ovate to lanceolate scales, these to 1 cm. long and 0.2-0.3 cm. broad; leaves crowded to fasciculate, mature ones to 1.5 m. long and 0.3 m. broad; petiole shorter than the lamina, yellowish, or reddish to grayish brown, subquadrangular, sulcate adaxially, near the base provided with brown scales, these lanceolate to ovate, to 1 cm. long, subentire; lamina pinnate, ovate, chartaceous to (more commonly) firm-membranaceous, glabrous, gradually terminating in a pinnatifid apex; rachis yellowish to grayish brown, essentially glabrous, but sometimes provided with minute, unicellular trichomes at the pinna axils, occasionally (outside Guatemala) provided with a proliferous bud in the axils of distal pinnae; pinnae 11-16 free pairs, most of them short-stalked, larger ones 12-16 cm. long, 2.5-3.5 cm. broad, oblong-lanceolate, acuminate at apex, broadly cuneate to truncate at base, the margin subentire to crenate-serrate; costa scarcely prominulous abaxially, commonly flattened adaxially, but often flanked by 2 slightly raised, parallel ridges of tissue, essentially glabrous; veins commonly distinct, light or dark brown, abaxially flush or slightly prominulous, pinnately branched, the branches 3-4 pairs, with tips of lower ones converging (or sometimes actually merging) with tips of adjacent branches at the pinna margin; sori relatively short (3-7 mm. long), commonly in 2-6 series on each side of the costa, borne subequally on both acroscopic and basiscopic vein branches; indusium narrow, scarious to light brown, ca. 0.3 mm. broad, and more constricted and darker brown at maturity.

***Diplazium verapax* (Donn.-Sm.) Hieron. Hedwigia 59: 322. 1917.**
Asplenium verapax Donn.-Sm. Bot. Gaz. 13: 77, t. 2. 1888 (type from Pansamalá, Alta Verapaz, *Tuerckheim s.n.* [ed. Donn.-Sm. No. 850]).

In rain forests, 970-1,200 m.; Alta Verapaz. Southern Mexico; Nicaragua; Panama; Puerto Rico.

Plants terrestrial; rhizome erect, sparsely provided at apex with inconspicuous, deep reddish brown, ovate scales 1-2 mm. long; leaves crowded to fasciculate, 40-80 cm. long, 5-13 cm. broad; petiole yellowish to light brown, nearly equaling or somewhat longer

than the lamina, sparsely scaly at base; lamina linear-lanceolate to narrow-ovate, consisting of 2-7 pairs of free pinnae toward the base, with the distal $\frac{1}{2}$ or $\frac{3}{4}$ pinnatifid or lobed to serrate, glabrous, firm-herbaceous to chartaceous; rachis yellowish to light brown, prominulous abaxially, broadly and shallowly sulcate adaxially, commonly bearing proliferous buds in the axils of a number of proximal pinnae; pinnae (free ones) 2-7 (9) cm. long, 1-2.5 cm. broad, ovate to lanceolate, subequilateral, the apex subacute to acute, the base cuneate to broadly rounded, the margins entire to serrate, proximal 1-3 pairs short-stalked, the rest sessile, becoming smaller and adnate up to the pinnatifid distal portion; veins in the pinnae 1- to 2- (3) forked, in the distal lobes pinnately branched with 3-4 pairs of branches; sori elongated, 0.4-1.5 cm. long, some mature ones often extending nearly from costa to margin; indusia scarious, yellowish or light brown, delicate, to 0.6 mm. broad, but commonly more constricted at maturity, some or many of them double.

With this must certainly be included *D. riedelianum* (Bong. ex Kuhn) Kuhn ex C. Chr., and perhaps *D. dissimile* Fée, both of Brazil. The former has been considered by some as synonymous with *D. verapax*, although Hieronymus (1917) suggested they be kept distinct on what are, to me, superficial and inconsistent features. I have not seen the type of either of the Brazilian species, but none of the specimens examined (so determined) differ much from those of *D. verapax*. Furthermore, nothing in either of the three descriptions points to any significant differences. Should comparison of all the types prove the three to be conspecific, then the name *D. riedelianum* would have priority.

Diplazium werckleanum Christ, Bull. Herb. Boissier II. 4: 969. 1904.

In wet forests, thickets, and wooded ravines, 800-2,500 m.; Alta Verapaz; Baja Verapaz; Chiquimula; Escuintla; Jalapa; Quezaltenango; El Quiché; San Marcos; Suchitepéquez; Zacapa. Southern Mexico to Panama.

Plants terrestrial; rhizome erect, provided at apex with ovate to linear-lanceolate scales, these dark brown to blackish, often lustrous, 1-3 mm. long; leaves crowded to fasciculate, 35-80 cm. long, 11-22 cm. broad; petiole 18-42 cm. long, equal to or often longer than the lamina, stramineous to light brown, subterete abaxially, sulcate adaxially, scaly near the base (the scales dark brown to blackish, 2-4 mm. long), otherwise glabrous; lamina pinnate, ovate or deltoid-ovate, firm-membranaceous to chartaceous, essentially glabrous, gradually terminating in a pinnatifid apex; rachis yellowish to grayish brown, glabrous, lacking a proliferous bud; pinnae 5-9 free pairs, most of them stalked, 6-14 cm. long, 1.5-3.5 cm. broad, deltoid-lanceolate, subfalcate, attenuate at apex, inequilateral at base (narrowly cuneate to excavate basiscopically, truncate and strongly produced acroscopically), serrate to crenate, or shallowly lobed, and then the lobes incised $\frac{1}{4}$ or less to the costa; costa glabrous, yellowish to greenish brown, slightly to strongly prominulous abaxially, adaxially flush, or immersed and flanked by raised, parallel, often cartilaginous ridges; ultimate segments (or crenations) commonly obtuse; veins distinct to indistinct, pinnately branched, not prominulous; sori in 1-4 series between costa and margin, that of the basal acroscopic vein branch longer and curved, the

others commonly shorter and straighter, usually only the basal one double; indusium linear, ample, light to dark brown, persistent or subsistent.

It is possible this may be only a variety of *D. cristatum*, under which see further discussion.

DORYOPTERIS J. Smith

REFERENCES: R. M. Tryon, A revision of the genus *Doryopteris*, Contr. Gray Herb. 143: 1-80. 1942.

Plants small to medium-sized, terrestrial or epipetric; rhizome erect to ascending (in ours) to long-creeping, scaly, the scales concolorous or (more commonly) bicolorous, usually less than 1 cm. long; leaves monomorphic or slightly dimorphic (the sterile ones in some species somewhat smaller than the fertile), crowded to subcaespitose; petiole long, not articulate, terete, or flattened to angled or winged adaxially, glabrous to minutely but amply pubescent, and sometimes sparsely scaly, often lustrous, castaneous to atropurpureous or blackish, often bearing proliferous buds at the base of the lamina; lamina essentially glabrous, firm-herbaceous to subcoriaceous, much shorter than the petiole, typically pedate, but in some species entire to 3-lobate or palmate; venation free, or partially to fully areolate, but without included free veinlets; sporangia long-stalked, commonly borne in continuous soral lines along the margins of segments; indusium reflexed, continuous along the soral line, formed by the greatly modified segment margin; paraphyses lacking; spores trilete, tetrahedral, with or without perine.

This small genus is very closely related (via the free-veined species) to *Cheilanthes*, under which see further discussion. As construed here there are about 25 species of *Doryopteris*, occurring in tropical regions around the world—the greatest number found in the neotropics. The genus is not common in Guatemala, but the following representatives have been reported there.

- a. Venation areolate; petiole amply but minutely puberulent (at least adaxially), bearing proliferous buds at the base of the lamina. *D. pedata* var. *palmata*.
- a. Venation free; petiole essentially glabrous (or with a few scales toward the base), lacking proliferous buds. *D. concolor*.

Doryopteris concolor (Langsd. & Fisch.) Kuhn in v.d. Decken, Reisen in Ost-Afrika 3 (3): 19. 1879. *Pteris concolor* Langsd. & Fisch. Icon. Fil. 19. 1810. *Pellaea concolor* (Langsd. & Fisch.) Baker in Mart. Fl. Brasil 1 (2): 396. 1870.

In forests or clearings, on the forest floor or on rock walls or rocky banks, 850-1,000 m.; Jutiapa. Southern Mexico; Honduras; El Salvador; West Indies; Colombia and Venezuela, south to Uruguay and Argentina; Old World tropics.

Plants terrestrial or epipetric; rhizome erect, amply provided with linear scales 1-2 mm. long, bicolorous, scarious to light brown, with a castaneous or blackish median stripe; leaves monomorphic or essentially so, 10-25 (-30) cm. long, 4-12 cm. broad; petiole 5-20 cm. long, 0.08-0.15 cm. thick, scarcely to highly lustrous, castaneous to atropurpureous, terete abaxially, somewhat flattened and often shallow-sulcate adax-

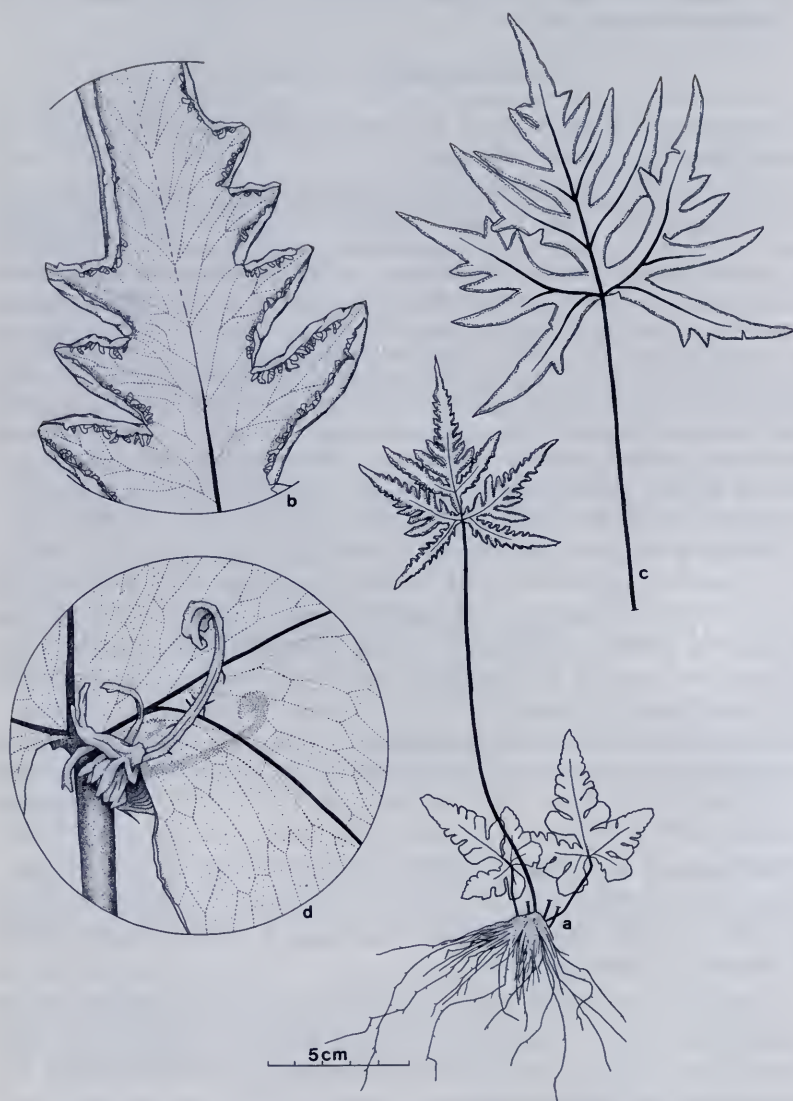


FIG. 27. *Doryopteris*. a-b, *D. concolor* var. *concolor*: a, habit, $\times \frac{1}{2}$; b, portion of pinna with veins and sori, $\times 6$; c-d, *D. pedata* var. *palmata*: c, leaf, $\times \frac{1}{2}$; d, base of lamina, showing venation and proliferous bud, $\times 3$.

ially, essentially glabrous, but often with a few scattered scales toward the base; lamina pedate, pentagonal, deeply pinnatifid or 2-pinnatifid (or 3-pinnatifid as to enlarged basal segments), tissue firm-herbaceous to chartaceous and essentially glabrous; primary segments commonly acute, the basal pair always the largest and most deeply lobed, the margins entire to crenate, costae and costules abaxially prominulous, lustrous, castaneous to blackish; venation free, obscure, the veins forked to pinnately branched, the tips nearly reaching the segment margin, and on sterile laminae ending in (usually) conspicuous hydathodes adaxially; soral lines continuous along the margins of primary segments, except commonly interrupted at tip and sinus; indusium subentire (in ours), scarious to yellowish or light brown.

The species is represented in the New World by var. *concolor*; var. *kirkii* (Hook.) Fries occurs in India and Africa. The latter is distinguished primarily by the sori and indusia being discrete, rather than continuous.

Besides the differences noted in the key, *D. concolor* can often be distinguished from *D. pedata* var. *palmata* (the only other Guatemalan species) by its smaller size. *Doryopteris concolor* rarely has leaves longer than 25 cm. long, with rhizome scales 1-2 mm. long. Leaves of *D. pedata* are commonly 30-50 cm. long, and rhizome scales are often 3-5 mm. long.

***Doryopteris pedata* (L.) Fée var. *palmata* (Willd.) Hicken**, Revista Mus. La Plata, Secc. Bot. 15: 253. 1908. *Pteris palmata* Willd. Sp. Pl. 5: 357. 1810. *D. palmata* (Willd.) J. Sm. J. Bot. (London) 4: 163. 1841. *Litobrochia palmata* (Willd.) Moore, Index Fil. 342. 1862. *Pteris pedata* L. var. *palmata* (Willd.) Baker in Martius, Fl. Brasil 1 (2): 408. 1870. *D. pedata* (L.) Fée ssp. *palmata* (Willd.) Hassl. Trab. Mus. Farm. Fac. Ci. Med. Buenos Aires 21: 20. 1909 (as *Dryopteris*).

Apparently represented thus far in Guatemala by a single collection: *Steyermark 37616*, dry slopes near Rio Cabús, Volcán Tajumulco, alt. 1,000-1,300 m., Dept. San Marcos. Southern Mexico; Nicaragua; Costa Rica; Panama; Colombia and Venezuela to Bolivia.

Plants terrestrial; rhizome erect, amply provided with linear to lanceolate scales, these 2-5 mm. long, bicolorous, light brown with a castaneous or blackish median stripe; leaves monomorphic or subdimorphic (the fertile leaves sometimes somewhat larger than the sterile and with more numerous segment lobes), 20-60 cm. long, 9-19 cm. broad; petiole 12-48 cm. long, 0.12-0.25 cm. thick, lustrous, castaneous to atropurpureous or blackish, abaxially terete and glabrous to sparsely puberulent, adaxially terete to somewhat flattened and amply but minutely puberulent; lamina pedate, deltoid or pentagonal, deeply pinnatifid, mature ones 2-pinnatifid as to the basal segments (occasionally 3-pinnatifid), chartaceous to subcoriaceous, glabrous, or sometimes with a few widely scattered filiform scales on or near the axes, abaxially; primary segments commonly acute, the basal pair always the largest and most deeply lobed, the margins entire (or sterile ones narrow-crenate or -crenulate), costae and costules abaxially prominulous,

lustrous, castaneous to blackish; venation areolate, lacking free included veinlets, but with vein tips free, these nearly reaching the segment margin, and on sterile laminae ending in conspicuous hydathodes adaxially; soral lines continuous from segment tips around the sinus, or often interrupted at the sinus; indusium subentire, occasionally slightly undulate, scarious to pale yellow or greenish.

The typical variety of *D. pedata*, from the West Indies, differs from var. *palmata* primarily in the lack of proliferous buds at the base of the lamina. Furthermore, the petiole in var. *pedata* is commonly strongly flattened adaxially, with the margins thus more sharply angled, even winglike.

DRYOPTERIS Adanson

REFERENCES: Carl Christensen, Subgenus I, *Eudryopteris* (pp. 64-73) in: A monograph of the genus *Dryopteris*, Part I . . . Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 55-282. 1913; and, Subgenus VII, *Eudryopteris*, (pp. 27-28) in: A monograph of the genus *Dryopteris*, Part II . . . *op. cit.* VIII. 6: 1-132. 1920.

Plants terrestrial or epiphytic; rhizome stout, erect or obliquely ascending, amply provided with entire to denticulate or fimbriate scales; leaves monomorphic, short- or long-petiolate, fasciculate; petiole not articulate, scaly (at least basally) as on the rhizome, abaxially rounded, adaxially sulcate; lamina decompose, often 3- to 4-pinnate, eglandular or variously beset with sessile or capitate glands, essentially glabrous, but the major axes sometimes sparsely to amply provided with scales, firm-herbaceous, oblong, ovate, subdeltoid, or occasionally pentagonal due to the basiscopically produced basal pinnae, tapering to a pinnatifid apex, lacking a proliferous bud on the rachis; rachis narrowly sulcate adaxially, with the raised, parallel ridges continuous as ridges on the costae; pinnae usually many, spreading to ascending, frequently asymmetrical, with pinnules (especially basal ones) on one side of the costa much larger than those of the other side, costae adaxially sulcate as on the rachis, with the raised ridges continuous as ridges along the costule; pinnules commonly anadromous at least on the basal pinnae, but often catadromous or subopposite on more distal pinnae; ultimate segments (in ours) not spinulose; venation commonly anadromous in the segments, veins free, rarely simple, usually 1-forked to pinnately branched; sori abaxial on the veins, commonly borne (at least in ours) on the vein branches; indusium subpersistent, often glandular, circular- to orbicular-reniform, attached at the sinus; paraphyses lacking; sporangium long-stalked, glabrous, glands present or lacking on the pedicel; spores monolete, bilateral, with perine.

For nearly a century, through the time of Christensen's treatment of 1920, *Dryopteris* was an extremely variable and broadly conceived genus. During this period, authors circumscribed within it the species of such genera as *Ctenitis*, *Thelypteris*, *Stigmatopteris*, *Lastreopsis*, and others. However, in the past 3 or 4 decades, the relationships of most of these taxa have been diligently explored, with the result that generic limits are now more clearly defined. *Dryopteris*, as herein

recognized, is a cosmopolitan genus of 150-180 species, occurring in temperate or tropical regions, with especially strong representation in China and Japan. These handsome ferns are typically deep forest plants, with highly divided leaves.

- a. Lamina pinnate-pinnatifid, or sometimes 2-pinnate as to bases of larger pinnae.
 - b. Rachis densely provided with dark-brown scales; pinnae with parallel sides in the proximal half, all the basal and middle segments subequal; most segments truncate at apex. *D. parallelogramma*.
 - b. Rachis sparsely or moderately provided with yellowish to light-brown scales; pinnae tapering from base to apex, the basal acroscopic segment much longer than the others; most segments rounded to subacute at apex. *D. filix-mas*.
- a. Lamina 2-pinnate to 3-pinnate (at least toward the base of the lamina).
 - c. Leaves copiously mealy-glandular throughout; indusium subglobose, persistent. *D. karwinskyana*.
 - c. Leaves minutely (if at all) capitate-glandular; indusium flat, often strongly contracting.
 - d. Lamina 3- to nearly 4-pinnate; petiole equal to or slightly longer than the lamina; basal basiscopic pinnules of basal pinnae much larger than the acroscopic ones.
 - e. Pinnae spreading at broad (nearly 90°) angles from the rachis; tissue firm-membranaceous to chartaceous; petiole scales scattered to ample. *D. nubigena*.
 - e. Pinnae (at least middle and lower ones) strongly ascending; tissue thin-membranaceous; petiole scales abundant (especially near the base). *D. futura*.
 - d. Lamina 2-pinnate-pinnatifid (never fully 3-pinnate); petiole commonly $\frac{1}{4}$ - $\frac{1}{2}$ as long as the lamina; basal basiscopic pinnules equal to or somewhat smaller than acroscopic ones.
 - f. Lamina finely (though minutely) capitate-glandular throughout; pinnae and pinnules mostly symmetrical, or nearly so. *D. patula* var. *patula*.
 - f. Lamina eglandular (or just sparsely so on rachis and base of costa); pinnae and pinnules mostly asymmetrical, their bases subtruncate and broader acroscopically, obliquely cuneate and narrower basiscopically. *D. patula* var. *serrata*.

Dryopteris filix-mas (L.) Schott, Gen. Fil. t. 67. 1834. *Polypodium filix-mas* L. Sp. Pl. 1090. 1753. *Nephrodium filix-mas* (L.) Rich. Cat. Pl. Jard. Med. Paris: 129. 1801.

In wooded ravine of *Juniperus standleyi*, alt. 3,400-3,500 m., Sierra de los Cuchumatanes, Huehuetenango (*Steiermark 48409*). Presumably known in Guatemala only from this collection. British Columbia to Newfoundland, southwest to Michigan, South Dakota and southwestern United States; rare in Mexico; Greenland and Eurasia.

Rhizome decumbent or erect, densely covered with scales, these orange or light brown, lanceolate to ovate, often with tortuous, filiform tips; leaves erect, caespitose, to 80 cm. tall and 25 cm. broad; petiole relatively short, 5 cm. (in ours) to 20 cm. long, light brown to stramineous, sparsely to amply provided with yellowish or light-brown, attenuate, ovate to lanceolate scales, these often with widely spaced teeth or cilia on the



FIG. 28. *Dryopteris*. a-b, *D. parallelogramma*: a, habit, $\times \frac{1}{2}$; b, pinna base with scales and sori, $\times 3$; c, *D. filix-mas*, pinna, $\times 1\frac{1}{2}$; d, *D. nubigena*, pinna $\times \frac{1}{2}$.

margins; lamina pinnate-pinnatisect to nearly bipinnate, firm-herbaceous, essentially glabrous, but filiform-scaly on costae and segment midribs abaxially, often darker colored adaxially than abaxially, lanceolate, tapered gradually to a pinnatifid apex, somewhat reduced at base; rachis light brown or stramineous, sparsely to amply provided with whitish or yellow, filiform, toothed or ciliate scales; pinnae numerous, approximate to subdistant, spreading or slightly ascending, short-stalked, narrow-deltoid, tapered gradually from base to pinnatifid apex, cut deeply or nearly quite to the costa; costa sparsely scaly abaxially, somewhat raised abaxially, essentially plane adaxially, but appearing very slightly sulcate toward pinna base adaxially; ultimate segments numerous, spreading at broad (but not right) angles to the costa, oblong, obtuse to subacute, broadly serrulate to crenate (rarely deeply so), sharply serrate apically, the basal acroscopic one obviously the longest; venation anadromous, veins oblique, mostly 1-forked from the midrib, running to the margin; sori 2-8 to a segment, borne on vein branches commonly in the basal half of the segments, medial or inframedial between midrib and margin; indusium glabrous, orbicular-reniform, persistent.

Although this is a species of temperate regions, it has been found on rare occasions in very high montane situations in Mexico and Guatemala. It is easily distinguished from *D. parallelogramma* by the characters noted in the key, but the two are rather closely related in many other respects, especially in characteristics of scales and indusia, and leaf outline and dissection. Two other collections of the species were reported by Hemsley (Biol. Centr. Amer. 3: 647. 1885): *Hartweg 570*, *Salvin & Godman s.n.* I have not seen these, and it is conceivable that they constitute additional records of *D. filix-mas* for Guatemala. It is equally likely that they are *D. parallelogramma*, a species Hemsley considered a variant of *D. filix-mas*.

Dryopteris futura A. R. Smith, Proc. Calif. Acad. Sci. 40: 216. 1975.

Río Zacualpa, 1,500 m., El Quiché, *Heyde & Lux s.n.* (ed. Donn.-Sm. 4663). Presumably known in Guatemala only from this collection. Mexico (Chiapas).

Rhizome not seen; leaves erect, to 75 cm. long and 27 cm. broad, scarcely glandular; petiole 30-45 cm. long, equal to or slightly longer than the lamina, drying light brown to stramineous, darker toward the base, abundantly provided with broad, dark-brown scales, and often muricate due to the persistent scale bases; lamina 3-pinnate to nearly 4-pinnate, thin-herbaceous, deltoid, tapering to a gradually pinnatifid apex, broadest at base; pinnae usually 10-12 pairs, crowded or imbricate, lower and middle ones stalked and strongly ascending, deltoid; costae and costules abaxially rounded, adaxially flanked by raised, cartilaginous ridges which are decurrent onto the axis of the next order below; pinnules 2-pinnatifid, spreading at nearly right angles to the costa, the proximal basiscopic ones larger than the acroscopic ones on lower pinnae, anadromous on basal pinnae and mostly catadromous on the others; tertiary segments pinnatifid to pinnatisect, the ultimate segments obtuse to acute; venation anadromous, veins oblique, pinnately branched in the segments, the branches often terminating short of the margin, their tips somewhat enlarged; sori borne near tips of veins near the segment margin; indusium relatively large, thin, flat, minutely capitate-glandular, persistent.

Dryopteris karwinskyana (Mett.) O. Ktze. Rev. Gen. Pl. 2: 813. 1891. *Aspidium karwinskyanum* Mett. Phleg. u. Aspid. 141. 1858. *Nephrodium karwinskyanum* (Mett.) Bak. in Hook. & Bak. Syn. Fil. 279. 1867.

On wet, shaded (often rocky) slopes and banks of ravines, in forests, 750-1,500 m.; Jutiapa; Santa Rosa; Zacapa. Mexico; Honduras; El Salvador; Nicaragua; Costa Rica.

Rhizome erect or ascending, densely covered with scales, these orange or light brown, lanceolate, attenuate, often with scattered teeth or cilia on the margin; leaves erect, approximate or fasciculate, to 70 cm. long and 20 cm. broad, copiously mealy-glandular throughout, the glands whitish, yellowish, or light brown, to 0.1 mm. long; petiole 10-20 (30) cm. long, light brown to stramineous, amply provided with scales as on the rhizome; lamina nearly 3-pinnatisect, herbaceous, sparsely to amply scaly along the axes, subdeltoid, tapered gradually to a pinnatifid apex, scarcely or not at all reduced at base; pinnae 12-18 pairs, crowded or imbricate, spreading at broad (nearly right) angles to the rachis, commonly short-stalked, lanceolate to ovate or subdeltoid, cut nearly or quite to the costa, the latter commonly narrow-alate for most of its length, rounded and slightly raised abaxially, essentially plane adaxially; pinnules deeply pinnatisect, spreading at nearly right angles to the costa, the proximal basiscopic ones much larger on basal pinnae than the acroscopic ones, anadromous on the basal pinnae, mostly catadromous or subopposite on the others; ultimate segments obtuse, broadly serrate, at least near the apex; venation anadromous, veins oblique, pinnately branched in the segments, branches running fully to the margin, their tips scarcely enlarged; 4-10 sori confined to the proximal half of each pinnule, commonly a single sorus to a segment, borne on the basal acroscopic branch of the vein; indusium orbicular-reniform, persistent, dark brown at maturity, usually covering the sorus, densely (almost bristly) glandular, the glands distinct, often whitish.

The thick, subglobose indusia and copious, meal-like glands provide a combination of characters which readily distinguish *D. karwinskyana* from any other species.

A strange plant was collected in Santa Rosa by Heyde & Lux (ed. Donn.-Sm. 6407) which matches no other species in our area. The lamina is 2-pinnate, with pinnules deeply pinnatisect, and all axes spread at nearly right angles to the axis on which each is borne, thus superficially resembling *D. karwinskyana*. However, the meal-like glands of the latter are lacking, segments are much broader, and the indusia are thin and flat, not thick and vaulted. Spores are abortive, and it is possible that this is a hybrid, with *D. karwinskyana* as one of the parents, and perhaps a variety of *D. patula* the other. Another Heyde and Lux specimen (ed. Donn.-Sm. 6405) collected in the same location is typical *D. karwinskyana*, and yet another (ed. Donn.-Sm. 6408) is *D. patula* var. *serrata*, so it is apparent that these and the putative hybrid were all growing together.

Dryopteris nubigena Maxon & Morton, Proc. Biol. Soc. Wash. 50: 179. 1937.

Terrestrial, on moist, shaded slopes and banks of ravines, often on mossy logs, in forests, 1,600-3,500 m.; Chimaltenango (type from Tecpam, *Sketch 771*); Huehuetenango; El Progreso; San Marcos; Sololá; Totonicapán. Costa Rica.

Rhizome ascending, densely covered with scales, these firm, lustrous, dark brown, lanceolate to ovate, minutely glandular-denticulate, acuminate; leaves suberect, approximate or subfasciculate, to 85 cm. long and 35 cm. broad, minutely capitate-glandular throughout; petiole to 50 cm. long, equal to or longer than the lamina, drying light brown (rarely stramineous) but becoming deep brown to atropurpureous toward the base, sparsely provided with broad, dark-brown scales, and often somewhat muricate due to the persisting scale bases; lamina nearly 3-pinnate to nearly 4-pinnate, firm-membranaceous to chartaceous, scaleless or essentially so, deltoid, tapered gradually to a pinnatifid apex, broadest at base; pinnae 9-15 pairs, crowded or imbricate, spreading at broad (often right) angles to the rachis, commonly short-stalked, narrowly or broadly deltoid, the costae very narrow-alate or those of lower pinnae completely free; costae and costules abaxially rounded, adaxially flanked by raised, cartilaginous ridges which are decurrent onto the axis of the next order below; pinnules 2-pinnatifid, spreading at right angles to the costa, the proximal basiscopic ones much larger than the acroscopic ones on basal pinnae, anadromous on the basal pinnae and mostly catadromous on the other; tertiary segments subopposite, pinnatifid to pinnatisect, the ultimate segments obtuse to acute; venation anadromous, veins oblique, pinnately branched in the segments, the branches often terminating short of the margin, their tips somewhat enlarged; sori borne near tips of vein branches near the segment margin; indusium relatively small, thin, flat, minutely capitate-glandular, strongly contracting at maturity.

Dryopteris parallelogramma (Kunze) Alston, Amer. Fern J. 47: 92. 1957. *Aspidium palaeaceum* Sw. Syn. Fil. 52. 1806 (not D. Don. 1825). *A. parallelogramma* Kunze, Linnaea 13: 146. 1839. *Nephrodium filix-mas* (L.) Rich. var. *parallelogramma* Hook. Sp. Fil. 4: 116. 1862. *D. palaeacea* (Sw.) C. Chr. Amer. Fern J. 1: 94. 1911 (not Hand.-Mazz. 1908) *nom. illeg.*

On the floor of dense, mixed or coniferous forests, often on slopes or in ravines, 2,200-3,800 m.; Chimaltenango; Huehuetenango; Jalapa; El Progreso; Quezaltenango; El Quiché; Sacatapéquez; San Marcos; Sololá; Totonicapán. Greater Antilles; Mexico to Argentina.

Rhizome erect, densely covered with scales, these orange or reddish brown, linear to lanceolate, with tortuous, filiform tips; leaves erect, rigid, densely caespitose, to about 1 m. long and 0.3 m. broad; petiole relatively short, to 0.25 m. long, light brown to stramineous, amply provided with dark-brown, linear or hairlike scales, these often with widely spaced teeth or cilia on the margin and dark-streaked in the center; lamina pinnate-pinnatisect to nearly 2-pinnate, chartaceous, sparsely scaly on both sides, commonly darker colored adaxially than abaxially, broadly or narrowly lanceolate, tapered

gradually to a pinnatifid apex, slightly reduced at base; rachis stramineous, with scales like those of the petiole, but darker (sometimes blackish), narrower and more copious; pinnae numerous, crowded, spreading at broad (commonly right) angles to the rachis, sessile or subsessile, oblong-lanceolate, their sides parallel for half their length, then tapering gradually to a pinnatifid, often attenuate apex, cut deeply or nearly quite to the costa; costa sparsely scaly on both sides, rounded and raised abaxially, plane adaxially, but commonly appearing immersed due to the presence of raised, flanking, cartilaginous ribs, which are essentially parallel to the costa but which often diverge slightly at the juncture with segment midribs; ultimate segments numerous, spreading at broad (nearly right) angles to the costa, strictly parallel to each other, oblong or oblong-rectangular, truncate or broadly rounded at the apex, subentire (rarely crenate), or serrulate (especially apically), the basal pair often basiscopically auriculate, the auricles overlapping the rachis; venation anadromous, veins oblique, 1- or 2- branched, running to the margin; sori 4-10 to a segment, borne on shortened vein-branches, commonly inframedial between midrib and margin; indusium glabrous, orbicular-reniform, persistent.

***Dryopteris patula* (Sw.) Underw., Our Native Ferns ed. IV: 117. 1893.**

Rhizome erect or ascending, densely covered with scales, these spreading to appressed, light brown, orange or reddish brown, subentire to remotely denticulate, lanceolate or linear-lanceolate, long-attenuate with an often filiform, tortuous tip; leaves erect, caespitose; petiole to 20 cm. long, much shorter than the lamina, drying stramineous or light brown, though sometimes somewhat darker at base, sparsely scaly above and more densely so at base; lamina 2-pinnate-pinnatifid to nearly 3-pinnate, thin- to firm-herbaceous, lanceolate or narrow-ovate to subdeltoid, tapering to a gradually pinnatifid apex, scarcely reduced at base; rachis stramineous or light brown, scales rare or lacking; pinnae 12-20 pairs, remote or sometimes crowded, spreading to strongly ascending, short-stalked, lanceolate to narrowly deltoid, costae marginate or narrowly alate, or nonalate on larger pinnae; costae and costules abaxially rounded, adaxially plane or slightly immersed, the proximal portions often flanked by slightly raised tissue forming faint ridges which may be decurrent onto the axis of the next order below; pinnules spreading obliquely from the costa, commonly (but not always) anadromous throughout, basal acroscopic and basiscopic ones subequal in size; tertiary segments entire to serrate to basal ones occasionally lobed; venation commonly anadromous, veins oblique, evident to somewhat obscure, 1 to several times branched in the segments, terminating near the margin, their tips not or scarcely enlarged; sori borne about midway along the abaxial vein branch; indusium thin, flat, finely or densely capitate glandular, strongly contracting at maturity.

A number of varieties of *D. patula* have been proposed or suggested by Christensen (1913) and other authors, but as of this time the taxonomy still remains greatly confused. In his treatment of *Dryopteris*, Christensen was somewhat vague about the geographic distribution of typical *D. patula*, except to mention that it occurred in Brazil and Jamaica. With this was contrasted var. *chaerophylloides* Moritz ex Mett. (= var. *serrata*), an eglandular variety from Central and South America, and Christensen's new var. *rossii* from Arizona and Mexico,

differing from the typical by its asymmetrical pinnae and pinnules and its lighter colored abaxial surfaces. *Dryopteris patula* var. *serrata* is the most widespread variety, ranging from southern Mexico to Bolivia. A number of specimens I have examined from Guatemala and Honduras match Christensen's description of var. *patula* and the Jamaican and Brazilian material he cited. However, study of other available neotropical collections reveals that var. *patula* (*sensu* Christensen) apparently does not occur between Honduras and Brazil! Christensen (*tom. cit.*) listed four more species and suggested (but did not fully describe) four other "forms," all of which apparently belong to one large species complex encompassed by *D. patula*. A detailed comparison of all the components of this complex is needed, and would be an interesting and enlightening study.

***Dryopteris patula* var. *patula*.** *Aspidium patulum* Sw. Kongl. Vetensk. Acad. Handl. 64. 1817. *Lastrea patula* (Sw.) Moore, Index Fil. 99. 1857. *Nephrodium patulum* (Sw.) Bak. Fl. Bras. 1 (2): 480. 1870.

Commonly terrestrial, among rocks, in shaded ravines or along river banks or in rock crevices, 900-1,600 m.; Chiquimula; Huehuetenango; Jalapa. Honduras; Brazil; Jamaica.

Leaves to 0.8 m. long and 0.25 m. broad; the axes and surfaces (especially adaxially) amply provided with minute, capitate glands; most of the pinnae and pinnules symmetrical or nearly so.

Dryopteris patula* var. *serrata (Mett.) Morton, Contr. U.S. Natl. Herb. 38: 219. 1973 (not *D. serrata* [Cav.] C. Chr. 1905). *Aspidium mexicanum* Kunze var. *serratum* Mett. Abh. Senckenberg Naturf. Ges. 2: 349. 1858. *A. chaerophylloides* Moritz ex Mett. *loc. cit.* *Nephrodium mexicanum* Hook. beta *A. chaerophylloides* Mortiz, in Hook. & Bak. Syn. Fil. 276. 1868. *A. patulum* Sw. var. *chaerophylloides* Bomm. & Christ, Bull. Soc. Roy. Bot. Belgique 35 (1): 214. 1896. *D. patula* var. *chaerophylloides* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 71. 1913 (not *D. chaerophylloides* [Poir.] C. Chr. 1920).

Terrestrial or, more commonly, growing on tree trunks or logs (in Honduras often collected on wet or mossy rocks), 350-2,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; El Quiché; Santa Rosa; Suchitepéquez. Southern Mexico; Honduras to Colombia and Venezuela, southward to Bolivia.

Larger leaves to 1.25 m. long and 0.4 m. broad, lamina essentially eglandular (though some capitate glands are sometimes found scattered along the rachis or at costa bases); pinnae commonly asymmetrical, often subdimidiate, their bases subtruncate and broader acroscopically, obliquely cuneate and narrower basiscopically.

ELAPHOGLOSSUM Schott ex J. Smith

JOHN T. MICKEL

New York Botanical Garden

REFERENCE: J. T. Mickel and L. Atehortúa, The subdivision of the genus *Elaphoglossum*, Amer. Fern J. 70: 47-68. 1980.

Generally epiphytes in wet montane forests, a greater percentage terrestrial at high elevations; rhizome short- to long-creeping, rarely erect, slender to stout (1-15 mm. in diameter); rhizome scales orange to black, basally attached or peltate, entire to toothed; fronds 2-200 cm. long, erect, spreading, or pendent, simple (pedate in 1 South American species); stipe glabrous or scaly, sometimes also with minute glandular hairs; stipe long or very short, base often darker (phyllopodium) with abscission at its upper demarcation rather than at the rhizome; blade linear to ovate or oblanceolate, apex acuminate or caudate to obtuse, base rounded to long attenuate; midvein grooved adaxially, usually with scales of the stipe abaxially; veins generally free, rarely netted or with a marginal commissural vein, simple to 2-forked, ending near the margin; those stopping well short of the margin usually end in conspicuous hydathodes; blade scales may be different from those of the rhizome or stipe, abundant to lacking, often greatly reduced to appear as stellate hairs; fertile fronds longer or shorter than the sterile fronds but generally have narrower blades and proportionally longer stipes; fertile blade completely covered beneath with sporangia (acrostichoid sori); sporangia long-stalked, the annulus erect, interrupted by the stalk; paraphyses in some species but generally lacking; spores bilateral, monolete, most with high crests or low ridges, but some echinate or tuberculate without ridges or crests.

Most measurements are given in terms of maximum size, which is usually close to the mature size. Blade size, though, tends to be more variable, and the average size may be about $\frac{2}{3}$ of the maximum. Rhizome diameter is given, excluding the scale covering. The rhizome scales may be appressed or widely spreading and would too greatly distort rhizome diameter measurements were they included. Stipe bases are differentiated into evident phyllopodia in some but not all species. Blade texture is difficult to determine on the basis of dried material and is given only for those species in which it is clearly distinctive. Although the veins seem to run to the margin in some species, they end just short of it, leaving a pale, thin margin 0.5-1 mm. wide, which is often difficult to distinguish, especially in very coriaceous or heavily indumented fronds. This margin is more readily distinguished in the fertile fronds where it remains sterile in contrast to the acrostichoid sorus of the rest of the abaxial surface. Vein angles and intervein distances are measured at midleaf, halfway between the midvein and margin. The scales of the rhizome and blade are generally quite

distinct from one another, and on the stipe they intergrade or in some cases remain distinct and occur together. The blade scales, although basically the same type on adaxial and abaxial surfaces, are more highly dissected abaxially. In some this means longer teeth, but in more extreme cases they are reduced to stellate hairs or even to resinous dots. In subglabrous fronds, the blade scales are reduced further in size to minute stellate hairs that are visible only with a hand lens. On the fertile blade, the adaxial surface scales are similar to those of the sterile blade, but abaxially the scales are generally limited to the midvein and in only a few species are there scales among the sporangia. Another type of indument is the presence of minute, erect, glandular hairs, which are found in varying degrees on the stipe and occasionally on the blade in *E. lindenii*, *E. erinaceum*, and their relatives (*E. albomarginatum*, *E. tambillense*, *E. apodum*, *E. siliquoides*).

There are probably well over 500 species in the genus, about three-fourths of them occurring in tropical America. There are 38 species recognized in Guatemala, though our knowledge of them is far from complete. Several are known from only one or a few specimens. The genus is very difficult taxonomically. There are many species and few characters, and the genus has not been adequately treated with a usable subgeneric breakdown until recently. Variation of the characters—such as plant size, blade form, scale color, scale type—is not fully understood in terms of species delimitation. The characters lie mostly in the scales of the rhizome and blade. The fertile fronds add characters of relative size, intersporangial scales, and spore details, but virtually all the species can be identified on the basis of vegetative material. Unfortunately collectors are hesitant to collect sterile material, and thus many records have gone uncollected.

This treatment was based primarily on specimens at F, NY, and US, with some additional observations, especially on types, at BM, K, L, and P.

- a. Sterile frond bearing linear-lanceolate scales that are usually inrolled to appear hair-like (subulate), at least on the stipe but generally throughout the frond, and/or with veins ending in hydathodes.
- b. Blade scales dark brown or black, concentrated on the stipe, margin, and midvein with virtually none on the blade surface; hydathodes lacking.
- c. Blade broadly elliptic; apex obtuse; veins netted, obscure. *E. crinitum*.
- c. Blade linear-lanceolate to ovate-lanceolate; apex acute to acuminate; veins free, evident.
- d. Blade scales abundant. *E. erinaceum*.
- d. Blade scales very sparse to lacking.
- e. Rhizome scales maroon, bristle-like; blade lanceolate; apex caudate.
E. tambillense.

- e. Rhizome scales orange, straplike; blade ovate-lanceolate; apex acute to acuminate, rarely caudate. *E. albomarginatum*.
- b. Blade scales orange or brown, more or less evenly distributed on the blade, although scales of the surface may be much smaller than those of the midvein and margin; hydathodes evident or not.
- f. Blade linear, margin crenulate; marginal and midvein scales larger than those of the blade surface. *E. eximium*.
- f. Blade linear to lanceolate, margin entire; marginal and midvein scales not especially larger than those of the blade surface.
- g. Fronds 2-4, rarely to 8 cm. long. *E. piloselloides*.
- g. Fronds 8-80 cm. long.
- h. Blade linear; blade scales ca. 10 mm. long; veins obscure. *E. siliquoides*.
- h. Blade linear to ovate-lanceolate; blade scales to 6 mm. long; veins evident.
- i. Rhizome long-creeping; blade scales flat, not hairlike.
- j. Fronds linear, glabrous; rhizome ca. 1 mm. in diameter; rhizome scales round, peltate. *E. amygdalifolium*.
- j. Fronds linear-lanceolate, scaly; rhizome ca. 2 mm. in diameter; rhizome scales linear, basally attached. *E. chiapense*.
- i. Rhizome short-creeping; blade scales with inrolled margins, hairlike.
- k. Stipe essentially lacking, less than $\frac{1}{2}$ of the frond length; hydathodes lacking. *E. apodum*.
- k. Stipe conspicuous, $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length; hydathodes evident.
- l. Blade truncate to subcordate at base; fertile fronds with no scales among the sporangia.
- m. Blade ovate-lanceolate; apex caudate, base subcordate; spores crested. *E. lindenii*.
- m. Blade linear-lanceolate, apex acuminate, base narrowly truncate; spores echinate, lacking crests or ridges. *E. crinipes*.
- l. Blade cuneate at base; fertile frond with scales among the sporangia.
- n. Fronds small, 8-18 cm. long, 0.8-1.4 cm. broad; blade conspicuously scaly, linear to linear-lanceolate. *E. setosum*.
- n. Fronds 10-34 cm. long, 1.2-2.7 cm. broad; blade very sparsely scaly, lanceolate to linear-lanceolate. *E. lanceum*.
- a. Sterile frond virtually glabrous with only minute stellate hairs to densely scaly; scales various (broadly lanceolate or ovate, ciliate, stellate, round-peltate) but not subulate; hydathodes lacking.
- o. Scales present on blade and stipe.
- p. Blade scales strictly limited to margin and midvein, golden, round, entire. *E. decoratum*.
- p. Blade scales at least in part on the blade surface, variously colored, elongate and/or dissected, usually toothed or dissected.
- q. Abaxial surface with stellate hairs or resinous dots (other types may be present also).
- r. Rhizome scales orange, dull. *E. pilosum*.
- r. Rhizome scales castaneous to black, lustrous.
- s. Scales of stipe and adaxial blade surface round, peltate. ... *E. tectum*.
- s. Scales of stipe and adaxial blade surface ovate, lanceolate, or stellate.
- t. Blade apex obtuse; blade scales ovate, entire. *E. huacsaro*.
- t. Blade apex acuminate; blade scales lanceolate or stellate.

- u. Frond scales virtually all stellate, with only an occasional lanceolate scale on stipe or adaxial midvein. *E. stellatum*.
- u. Frond scales lanceolate on adaxial blade surface, abaxial midvein and stipe; scales lanceolate, stellate, and/or resinous dots on abaxial surface.
 - v. Scales of rhizome and stipe base entire; stipe ca. $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length; blade 10-30 cm. long. *E. petiolatum*.
 - v. Rhizome scales with short teeth; scales of stipe base deeply toothed; stipe $\frac{1}{4}$ - $\frac{3}{4}$ of the frond length; blade 4-9 cm. long. *E. gratum*.
- q. Abaxial surface lacking resinous dots and stellate hairs.
 - w. Blade 3-4.8 cm. broad, ovate-lanceolate to elliptic with obtuse tip; spores tuberculate.
 - x. Rhizome scales entire; stipe scales erose; blade scales with cilia shorter than the width of the scale body; rhizome short-creeping to erect. *E. muscosum*.
 - x. Rhizome scales ciliate; stipe scales ciliate; blade scales with cilia as long as the width of the scale body; rhizome moderately to short-creeping. *E. engelii*.
 - w. Blade 1-3.2 cm. broad, lanceolate or linear-lanceolate, apex acute to acuminate, rarely obtuse; spores with crests or ridges, not tuberculate.
 - y. Rhizome long-creeping. *E. mathewsii*.
 - y. Rhizome short-creeping.
 - z. Abaxial blade surface densely covered with scales, usually obscuring the veins and lamina.
 - aa. Blade 1.5-3.5 cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length. *E. paleaceum*.
 - aa. Blade less than 1.1 cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length. *E. dombeyanum*.
 - z. Abaxial blade surface scaly but veins and lamina evident.
 - bb. Stipe long, $\frac{1}{3}$ - $\frac{1}{2}$ of the frond length. *E. gratum*.
 - bb. Stipe short, $\frac{1}{8}$ - $\frac{1}{4}$ of the frond length.
 - cc. Rhizome scales orange with long hair-teeth; blade scale margins spreading; stipe $\frac{1}{8}$ - $\frac{1}{4}$ of the frond length. *E. auricomum*.
 - cc. Rhizome scales dark, entire, with short, weak teeth; blade scale margins turned up; stipe ca. $\frac{1}{4}$ of the frond length. *E. rubescens*.
 - o. Scales lacking on blade and stipe except in some cases for minute stellate hairs or a few scales at base of stipe.
 - dd. Rhizome 1-2 mm. in diameter, moderate- to long-creeping, the stipe bases 1-30 mm. apart; rhizome scales either uniform orange or tan or with irregular black streaks.
 - ee. Rhizome scales all orange or tan; phyllopodia lacking; plants epiphytic; fronds 4-8.5 cm. long.
 - ff. Blade spatulate. *E. squamipes*.
 - ff. Blade linear to linear-lanceolate. *E. revolutum*.
 - ee. Rhizome scales mostly tan but at least some with dark streaks; phyllopodia distinct; plants terrestrial or epipetric; fronds 8-30 cm. long.
 - gg. Blade 12-26 mm. broad; rhizome with stipes 3-30 mm. apart. *E. affine*.

- gg. Blade 6-10 mm. broad; rhizome with stipes 1-8 mm. apart.
E. tenuifolium.
- dd. Rhizome 2-10 mm. in diameter, short-creeping, the stipe bases 1-3 mm. apart; rhizome scales uniformly light or dark colored, never with irregular black streaks.
- hh. Veins with laterally expanded ends, sometimes joining; blade very thin, the veins easily seen. *E. acutissimum.*
- hh. Veins without laterally expanded ends, never joining; blades mostly coriaceous, with veins obscure.
- ii. Rhizome scales maroon-black, bristle-like.
- jj. Blade apex obtuse; veins obscure; stipe $\frac{1}{2}$ - $\frac{3}{4}$ of the frond length.
E. glaucum.
- jj. Blade apex caudate; veins evident; stipe $\frac{1}{3}$ - $\frac{1}{2}$ of the frond length.
E. tambillense.
- ii. Rhizome scales pale to brown, thin to stiff but not bristle-like.
- kk. Rhizome scales bright orange, 15-30 mm. long; blade bluish green, to 200 cm. long; plants of low elevation. *E. herminieri.*
- kk. Rhizome scales orange to dark brown, 3-10 mm. long; blade green, rarely bluish green, to 70 cm. long; plants mostly of medium to high elevation.
- ll. Blade ovate-lanceolate; base rounded; veins evident; blade thin, with an occasional subulate scale, especially when young.
E. albomarginatum.
- ll. Blade linear to linear-lanceolate or oblanceolate; base cuneate to long-attenuate; veins obscure; blade coriaceous; subulate scales never present.
- mm. Blade oblanceolate, base long-decurrent. *E. rigidum.*
- mm. Blade linear to linear-lanceolate, base cuneate but not long-decurrent.
- nn. Rhizome 4-10 mm. in diameter excluding scales; rhizome scales orange, tan, or dirty brown, rarely somewhat lustrous, never deciduous. *E. latifolium.*
- nn. Rhizome 2-4 mm. in diameter, excluding scales; rhizome scales lustrous dark brown, often deciduous, leaving a naked rhizome.
E. guatemalense.

Elaphoglossum acutissimum Christ, Bull. Herb. Boissier II. 5: 730. 1905.

On trees in wet forests, 1,300-2,500 m.; Alta Verapaz; Quezaltenango; Suchitepéquez; Zacapa. Southern Mexico (type from San Pablo, Chiapas, *Münch* 168).

Plants epiphytic; rhizome short-creeping, to 3 mm. in diameter; rhizome scales linear-lanceolate, lustrous, thin, brown, crisped, to 5 mm. long, entire; phyllopodia lacking; fronds clumped, to 74 cm. long, 4.5 cm. broad; stipe $\frac{1}{10}$ - $\frac{1}{5}$ of the frond length, clothed with minute, stellate, appressed hairs; blade linear, apex long-acuminate, base cuneate; very thin; veins evident, free, simple or 1-forked, 1.5-2 mm. apart, running at 60-70° angle; hydathodes lacking, but vein tips expanded laterally, sometimes uniting; blade scales lacking but minute, stellate, reddish resinous hairs present, mostly on the abaxial surface; fertile fronds about equal to the sterile in length, though with longer

stipe (ca. $\frac{1}{2}$ of the fertile frond length) and narrower blade; scales lacking from abaxial surface; spores with sparse, smooth ridges and small protuberances between the ridges.

This is distinct from other species by its very thin blade and laterally expanded vein ends. Specimens from Chiapas seem to have more resinous rhizome scales than do those of Guatemala and Oaxaca.

Elaphoglossum affine (Mart. & Gal.) Moore, Index Fil. 4. 1857. *Acrostichum affine* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 24, t. 3, f. 1. 1842 (type from Volcán Orizaba, Veracruz, Mexico, *Galeotti* 6454).

On ground among moss or in crevices of boulders in damp oak forests, 2,500-3,000 m.; Quezaltenango; San Marcos; Sololá. Mexico.

Plants terrestrial or epipetric; rhizome short- to long-creeping, 1-2 mm. in diameter; rhizome scales dense to sparse, ovate, orange with varying degrees of dark, shiny, sclerotic streaking, ca. 3 mm. long, deeply cordate and appearing nearly peltate, entire or with occasional small, irregular teeth; phyllopodia distinct; fronds spaced 3-30 mm. apart, to 30 cm. long, 2.1 cm. broad; stipe $\frac{1}{2}$ - $\frac{2}{3}$ of the frond length, glabrous except for the very base; blade linear-lanceolate, apex acute to acuminate, base cuneate; coriaceous; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales sparse; minute, stellate hairs on abaxial surface, more sparse adaxially; fertile fronds similar to the sterile in size and shape; scales lacking on abaxial surface; spores with small, narrow crests.

Specimens are usually well over 1 cm. broad, but *Standley* 86176 is only 0.8 cm. wide and might be confused with *E. revolutum*, which is always epiphytic and has no phyllopodia and no sclerotic streaks in the rhizome scales. *Elaphoglossum affine* also closely resembles *E. guatemalense*, which has a shorter rhizome, and rhizome scales are uniformly dark lustrous brown, not orange-tan with black streaks.

Although the general habit and the dark streaks of the rhizome scales are similar to those of *E. tenuifolium*, *E. affine* can be distinguished by its broader blade and to some extent by the generally longer creeping rhizome. It is also very closely related to *E. leptophyllum* (Fée) Moore of the West Indies and South America.

Elaphoglossum albomarginatum A. Reid Smith, Proc. Calif. Acad. Sci. (4th ser.) 40(8): 220. f. 4A. 1975.

On tree trunks and terrestrial on cliff faces and shaded slopes, 1,800-2,500 m.; El Progreso; Quezaltenango; San Marcos; Suchitupéquez. Southern Mexico (type from Talquian, Chiapas, *Breedlove & Smith* 31629).

Plants epiphytic, epipetric, or terrestrial; rhizome short-creeping, stout, to 10 mm. in diameter; rhizome scales orange to brown, ribbonlike or nearly hairlike, to 10 mm. long; phyllopodia lacking; fronds clumped, to 60 cm. long, 8.5 cm. broad; stipe $\frac{1}{3}$ - $\frac{1}{2}$ of the frond length, with spreading, subulate scales or glabrous, usually with minute, erect,

glandular hairs; blade ovate-lanceolate, apex acute to acuminate, rarely caudate, base rounded; veins evident, free, 1- or 2-forked, 1.5-2 mm. apart, running at 70-80° angle; hydathodes lacking; margin pale, ca. 0.5 mm. wide; blade completely lacking scales but with minute, black, stellate hairs; fertile fronds smaller than the sterile, with a conspicuous sterile margin (ca. 1 mm. wide); scales lacking on abaxial midvein and among sporangia; spores with relatively few slender ridges with some spicules on and between the crests.

This closely resembles a large specimen of *E. tambillense*, but differs not only in size but also in the rhizome scales and the pale, thin margin on both the sterile and fertile fronds. Marginal blade scales are lacking in *E. albomarginatum*, whereas in *E. tambillense* at least an occasional marginal scale is found.

Elaphoglossum amygdalifolium (Mett. ex Kuhn) Christ, Monogr. Elaph. 101, f. 53. 1899. *Acrostichum amygdalifolium* Mett. ex Kuhn, Linnaea 36: 41. 1869. *A. tatei* Hooker & Baker, Syn. Fil., ed. 2. 518. 1874.

On trees in wet forests, 1,350 m.; Alta Verapaz. Honduras; Nicaragua; Costa Rica; Cuba; Colombia.

Plants epiphytic; rhizome long-creeping, thin, 1 mm. in diameter; rhizome scales nearly round, peltate, dark brown; phyllopodia lacking; fronds distant, to 25 cm. long, 2 cm. broad; the stipe $\frac{1}{20}$ - $\frac{1}{6}$ of the frond length, sparsely clothed with appressed scales; blade linear to linear-lanceolate, apex acuminate, base narrowly cuneate, very thin; veins evident, simple or 1-forked, 1.5-2 mm. apart, running at 60-70° angle; hydathodes evident; blade glabrous except for a few roundish, peltate scales near the base of the midvein; fertile fronds shorter and narrower than the sterile, ca. 15 cm. long, 8 mm. broad, stipe ca. $\frac{1}{3}$ of the fertile frond length; scales lacking on abaxial surface; spores with slender crests and minute spicules on crest margins and on areas between the crests.

One of the most distinct species in the genus with its very long-creeping rhizome and thin, narrow blade. Rare in Guatemala, more abundant in southern Central America.

Elaphoglossum apodum (Kaulf.) Schott var. *latum* Mickel, Amer. Fern J. 69: 100. 1979.

On tree trunks in wet forests, 75-500 m.; Alta Verapaz (type from Semococh-La Laguna, *Steyermark 46368*); Izabal; Petén. Costa Rica; Hispaniola; Colombia.

Plants epiphytic; rhizome short-creeping, to 6 mm. in diameter; rhizome scales orange, linear, entire, to 10 mm. long; phyllopodia lacking; fronds clumped, to 36 cm. long, 5.5 cm. broad; stipe nearly lacking, to 1 cm. long, less than $\frac{1}{10}$ of the frond length, clothed with orange, spreading, subulate scales and minute, erect, glandular hairs; blade narrowly oblanceolate, base cuneate, narrowing very gradually to somewhat abruptly; apex long acuminate; papyraceous to coriaceous; veins somewhat obscure, free, 1- or 2-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales subulate, orange, especially concentrated on the midvein and margin, some scales on

abaxial blade surface, very sparse on adaxial surface; blade also with minute, erect, glandular hairs; fertile fronds much smaller than the sterile fronds (ca. $\frac{1}{2}$ as long, to 13 cm. long, 1 cm. broad) with linear orange scales on the abaxial midvein, lacking among the sporangia; spores with low, broad, smooth ridges.

The Central American and Colombian material is noticeably larger than that of typical *E. apodum* of the West Indies. It compares well with *Ekman H 13406* of Santo Domingo, which Ekman apparently thought was a new species, but Christensen, though he named the specimen var. *majus*, did not publish the name.

***Elaphoglossum auricomum* (Kunze) Moore, Index Fil. 7. 1857.**
Acrostichum auricomum Kunze, Linnaea 9: 28. 1834.

Pendent on tree trunks in wet forests, 1,250-1,650 m.; Alta Verapaz; Huehuetenango; Petén. Honduras; Costa Rica; Hispaniola; Colombia to Bolivia.

Plants epiphytic; rhizome short-creeping, to 5 mm. in diameter; rhizome scales linear-lanceolate, dark orange-brown, to 7 mm. long, margin with hairlike teeth; phyllopodia inconspicuous or lacking; fronds clumped, to 50 cm. long, 3.2 cm. broad; stipe $\frac{1}{8}$ - $\frac{1}{4}$ of the frond length, densely clothed with spreading, orange scales 4 mm. long; blade linear, apex acuminate, base narrowly cuneate, papyraceous; veins indistinct, free, simple or 1-forked, 1-2 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales orange, liberally distributed but not overlapping, linear-lanceolate, 1-4 mm. long with long, hairlike teeth, the teeth at least half as long as the scale, some scales reduced to nearly stellate hairs; fertile fronds rare, nearly as long as the sterile fronds but narrower and with longer stipes, stipes ca. $\frac{1}{2}$ of the fertile frond length, with a few stellate hairs on the abaxial midvein; spores with smooth crests and small protuberances on spore surface between crests.

This species is close to *E. vestitum* (Schlecht. & Cham.) Schott of Mexico in the skeletonized blade scales and the general laxness of the fronds, but differs in several features. The Guatemalan plant lacks the caudate blade tip, the rhizome scales are not as dark, and the stipe is densely covered with scales. It also resembles *E. paleaceum*, but the rhizome scales are dark orange or maroon, not black as usually found in *E. paleaceum*, and the blade scales are more sparse and more highly dissected than in that species. Some specimens have very short stipes, but apparently this character is quite variable in this species.

***Elaphoglossum chiapense* A. Reid Smith, Proc. Calif. Acad. Sci. (4th ser.) 40(8): 220, f. 4B-D. 1975.**

On moist banks and rocks, 2,400-2,700 m.; Quezaltenango; San Marcos. Southern Mexico (type from Rayón Mezcalapa, Chiapas, *Breedlove & Smith 32649*).

Plants terrestrial or epipetric; rhizome moderately to long-creeping, to 2 mm. in diameter; rhizome scales maroon, lustrous, linear, to 6 mm. long, short-toothed, especially along the elongate tip; phyllopodia lacking; fronds spaced apart, to 22 cm. long, 2.2

cm. broad; stipe $\frac{1}{5}$ - $\frac{1}{2}$ of the frond length; stipe scales linear, maroon, ca. 2 mm. long, toothed, appressed; blade linear-lanceolate, apex acute to acuminate, base cuneate; veins evident, free, simple or rarely 1-forked, 1.5-2.5 mm. apart, running at 50-60° angle; hydathodes evident; blade scales brown, linear-lanceolate with flared base, evenly and sparsely distributed on the blade, not noticeably along the margin, 2 mm. long, with short teeth; fertile fronds smaller than the sterile, fertile blade ca. 3.5 cm. long, 1.2 cm. broad; stipe ca. $\frac{1}{5}$ of the fertile frond length; scales lacking on the abaxial surface; spores with short crests and holes in the spore surface.

Elaphoglossum chiapense is known previously only from Chiapas. It resembles *E. lindenii* in the spores but differs in the longer creeping rhizome and the narrower blade. It closely resembles, if not equals, *E. alpestre* (Gardn.) Moore of South America, but *E. chiapense* does not have its blade scales inrolled.

Elaphoglossum crinipes C. Chr. Kongl. Svenska Vetenskapsakad. Handl. (ser. 3) 16 (2): 76, t. 17, f. 1-2. 1936.

Mostly on tree trunks, occasionally on rocks and most banks in wet forests, 1,800-3,000 m.; Alta Verapaz; Guatemala; Huehuetenango; El Progreso; Quezaltenango; San Marcos; Totonicapán. Southern Mexico; Costa Rica; Panama; Hispaniola.

Plants epiphytic, less commonly epipetric or terrestrial; rhizome short-creeping, to 9 mm. in diameter; rhizome scales linear-lanceolate, reddish orange, to 12 mm. long, with short teeth; phyllopodia lacking; fronds clumped, to 57 cm. long, 4 cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length; stipe scales reddish orange, spreading, subulate, slightly toothed, to 4 mm. long; blade linear-lanceolate, apex acuminate, base rounded, truncate, or broadly cuneate; veins distinct, free, simple or 1-forked, 1.5-2.5 mm. apart, running at 60-70° angle; hydathodes evident; blade scales abundant, reddish orange, subulate, slightly toothed, more dense at margin, spreading to 5-6 mm. long, usually less scaly on the adaxial surface; fertile fronds slightly shorter than the sterile, to 38 cm. long, 2.5 cm. broad, with longer stipe (ca. $\frac{3}{4}$ of the fertile frond length); fertile blade base subcordate, apex acute; scales lacking on abaxial surface; spores densely echinate, lacking ridges or crests.

This species closely resembles *E. villosum* (Sw.) J. Smith of the West Indies, but is distinct from it in that *E. villosum* has scales among the sporangia and the blade has a caudate apex and a more cuneate base.

Elaphoglossum crinitum (L.) Christ, Monogr. Elaph. 102, f. 53. 1899. *Acrostichum crinitum* L. Sp. Pl. 2: 1068. 1753. *Hymenodium crinitum* (L.) Fée, Mém. Fam. Foug. 2: 90. 1845.

On trees in wet forests, 800 m.; Alta Verapaz. Costa Rica; West Indies; Trinidad.

Plants epiphytic; rhizome short-creeping, to ca. 10 mm. in diameter; rhizome scales linear, crisped, orange, ca. 10 mm. long; phyllopodia lacking; fronds clumped, to 80 cm.

long, 22 cm. broad; stipe nearly as long as the blade, densely scaly, the scales very slender, subulate, dark brown; blade elliptical with rounded base and obtuse apex, coriaceous; veins obscure, netted, curving out from the midvein and mostly lying at ca. 55° angle; hydathodes lacking; scales on midvein and margin, sparsely on blade surfaces; fertile fronds much smaller than the sterile, the stipe $\frac{3}{4}$ - $\frac{3}{4}$ of the fertile frond length; scales lacking among the sporangia; spores with broad, smooth, low ridges.

This species is sometimes segregated from *Elaphoglossum* as a distinct genus, *Hymenodium*, on the basis of its netted veins and large, elliptical blade. It is certainly more distinct than most species, but not worthy of generic distinction, being allied closely to the *E. erinaceum* group. It is rare in Central America but frequent in the West Indies.

Elaphoglossum decoratum (Kunze) Moore, Index Fil. 8. 1857. *Acrostichum decoratum* Kunze, Linnaea 9: 25. 1835.

On trees in wet forests, 800-1,500 m.; Alta Verapaz. Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Peru.

Plants epiphytic; rhizome short-creeping, to 6 mm. in diameter; rhizome scales linear, orange, crisped, to 16 mm. long, entire or with very sparse, small, irregular teeth; phyllopodia lacking; fronds clumped, to 70 cm. long, 12 cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length; stipe scales orange, ovate, spreading, with obtuse tip, to 10 mm. long; blade elliptic, apex cuspidate, base broadly cuneate, thin; veins evident, free (with rare anastomoses), simple or 1-forked, ca. 2 mm. apart, running at ca. 70° angle; hydathodes lacking; blade scales limited to the midvein and margin, forming a continuous band of overlapping, cordate, golden scales on the margin, elliptic on the midvein; fertile fronds rare, shorter than the sterile fronds, margins lacking scales; spores with low, broad, smooth ridges.

The species is rare throughout its range.

Elaphoglossum dombeyanum (Fée) Moore & Houlst. Gard. Mag. Bot. 3: 95. 1851. *Acrostichum dombeyanum* Fée, Mém. Fam. Foug. 2: 59, t. 17, f. 2. 1845.

On trees in wet forests, 2,500-3,000 m.; San Marcos. Panama; Venezuela and Colombia, south to Bolivia.

Plants epiphytic; rhizome short-creeping, to 3 mm. in diameter, but heavily scaly and with stipe bases to appear thicker; rhizome scales linear-lanceolate, black to blackish maroon, ca. 5 mm. long, margin with hairlike teeth; phyllopodia distinct; fronds clumped, to 32 cm. long, 1.1 cm. broad; stipe $\frac{1}{3}$ - $\frac{1}{2}$ of the frond length, densely clothed with scales; stipe scales mostly appressed with some spreading, less than 1 mm. long, with hair teeth; blade linear-lanceolate, apex obtuse to acuminate, base narrowly cuneate; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales of abaxial surface abundant, overlapping, ovate-lanceolate, mostly orange, blackish on midvein, on adaxial surface orange to white, lanceolate, sparse; fertile frond about equal to the sterile but more often obtuse and broader, to 28 cm. long, 1.2 cm. broad; scales on the abaxial midvein; spores with low, broad, smooth or sparsely spiculate ridges.

It is closely allied to *E. paleaceum*, but the blades are smaller and narrower, the stipe scales are smaller and less spreading, and the stipe is relatively longer.

Elaphoglossum engelii (Karsten) Christ, Monogr. Elaph. 81. 1899. *Acrostichum engelii* Karsten, Fl. Col. 1: 118, t. 59. 1860.

On trees or rarely on the ground in wet forests, 3,000-3,500 m.; Alta Verapaz; Huehuetenango; Quezaltenango. Costa Rica; Hispaniola; Colombia to Bolivia.

Plants epiphytic, rarely terrestrial; rhizome short- to moderately creeping, to 4 mm. in diameter; rhizome scales linear, reddish orange, 8 mm. long, with long hair teeth; phyllopodia inconspicuous or lacking; fronds clumped to slightly spaced apart, to 30 cm. long, 4.2 cm. broad; stipe $\frac{1}{2}$ of the frond length; stipe scales broad, spreading, orange, ca. 2 mm. long, with long hair teeth; blade narrowly elliptic, apex obtuse, base broadly cuneate; subcoriaceous; veins obscure, free, simple or 1-forked, ca. 1.5 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales on adaxial surface white, lanceolate, with long hair teeth, on abaxial surface orange and overlapping; fertile fronds slightly longer than the sterile, narrower, with stipe $\frac{2}{3}$ of the fertile frond length; scales with long hair teeth, conspicuous and abundant among the sporangia; spores with very short tubercles.

This species is commonly mistaken for *E. muscosum*. See the comments under that species for distinguishing features.

Elaphoglossum erinaceum (Fée) Moore, Index Fil. 9. 1857. *Acrostichum erinaceum* Fée, Mém. Fam. Foug. 2: 41. 1845. *A. blepharodes* Fée, *tom. cit.* 48, t. 24, f. 3. 1845, cites *A. crinitum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 25. 1842 (type from Zacuapán, Veracruz, Mexico, *Galeotti 6297*), not L. 1753. *E. fimbriatum* Moore, Index Fil. 356. 1862, based on *A. nitidum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 168 (seors. 16). 1849 (type from Chinautla, Puebla, Mexico, *Liebmann 2421*), not *Elaphoglossum nitidum* Brack. 1854, not *Acrostichum fimbriatum* Sodiro, 1883. *E. blepharodes* (Fée) Moore, Index Fil. 7. 1857. *A. mexicanum* Fourn., Mex. Pl. 1: 63. 1872 (type from Chinautla, Puebla, Mexico, *Liebmann s.n.*).

On moist, rocky banks or on tree trunks in wet forests, 1,200-2,900 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Suchitepéquez; Zacapa. Southern Mexico; El Salvador; Honduras; Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Bolivia and Brazil.

Plants epiphytic, epipetric, or terrestrial; rhizome short-creeping, to 7 mm. in diameter; rhizome scales linear, orange, to 17 mm. long, entire or with very irregular teeth near the tip; phyllopodia lacking; fronds clumped, to 73 cm. long, 8.0 cm. broad; stipe $\frac{1}{3}$ - $\frac{1}{2}$ of the frond length; stipe scales dark reddish brown, subulate, widely spreading, to

5 mm. long, also with minute erect glandular hairs on stipe and midvein; blade lanceolate to elliptic, apex acuminate to caudate, base cuneate to rounded; veins evident, free, simple or 1-forked, 1-2 mm. apart, running at 70-80° angle; hydathodes lacking; blade scales subulate, dark reddish brown, often appearing black, mostly on the midvein and spreading from the margin; also minute simple, branched, or stellate hairs on the abaxial surface; fertile fronds considerably shorter than the sterile (ca. ½ the length of the sterile) and somewhat narrower, lanceolate to linear-lanceolate; with a noticeable sterile margin; scales lacking on the abaxial surface; spores with broad, low, smooth ridges.

Elaphoglossum erinaceum belongs to a very perplexing group. Although the Guatemalan material shows considerable variation in blade size, rhizome scale size, and habitat, the complex is much better represented in Mexico and South America.

***Elaphoglossum eximium* (Mett.) Christ, Monogr. Elaph. 107. 1899.** *Acrostichum eximium* Mett., Ann. Sci. Nat. Bot. V. 2: 199. 1864. *E. lineare* var. *klotzschii* Hieron. Bot. Jahrb. Syst. 34: 552. 1904. *E. cordigerum* Christ, Bull. Soc. Bot. Gèneve II. 1: 224. 1909.

On trees in wet forests, 1,000-2,200 m.; El Progreso; Santa Rosa; Zacapa. Southern Mexico; El Salvador; Honduras; Costa Rica; Panama; Colombia and Venezuela.

Plants epiphytic; rhizome short-creeping, ca. 5 mm. in diameter; rhizome scales dark, castaneous, lustrous, linear, entire, 3-5 mm. long; phyllopodia lacking; fronds clumped, to 32 cm. long, 1.7 cm. broad; stipe short, ca. ¼ of the frond length, densely clothed with short, brown, subulate scales; blade linear, apex acuminate, base attenuate; margin crenulate, thin; veins evident, free, mostly simple or 1-forked, rarely 2-forked, ca. 2 mm. apart, running at 45-50° angle; hydathodes evident; scales conspicuous but sparse on midvein, smaller on margin, mostly between crenulations, minute and inconspicuous on blade surfaces; fertile fronds shorter than the sterile, stipe ¾ of the fertile frond length; blade entire, lanceolate, base truncate to cordate, apex acute; scales lacking among sporangia; spores densely echinate.

This species belongs to an interesting complex with relatives in the West Indies, South America, and Africa. It is also closely related to the only pedate-bladed species, *E. cardenasii* Wagner, of Peru and Bolivia. Specimens of *E. eximium* are often mistakenly named *E. aubertii* (Desv.) Moore, which is of the same group but occurs in Africa.

***Elaphoglossum glaucum* (Fée) Moore, Index Fil. 10. 1857.** *Acrostichum glaucum* Fée, Mém. Fam. Foug. 8: 67. 1857 (type from Mexico, Veracruz, Cordoba, *Schaffner 16*, in 1854). *E. eucraspedum* Christ, Bull. Herb. Boissier II. 7: 415. 1907.

On trees in wet forests, 1,800-3,500 m.; Chimaltenango; Quezaltenango; Sololá; Totonicapán. Mexico (type from Chiapas, *Münch 1902*).

Plants epiphytic; rhizome short- to moderately creeping, ca. 5 mm. in diameter; rhizome scales linear-deltoid, hairlike most of their length, lustrous reddish brown to nearly black, to 17 mm. long, entire; phyllopodia distinct; fronds clumped or spaced a few mm. apart, to 62 cm. long, 3.8 cm. broad, though usually much smaller; stipe $\frac{1}{2}$ - $\frac{3}{4}$ of the frond length, glabrous; blade linear-lanceolate, apex acute to obtuse, base cuneate, coriaceous; veins obscure, free, curved, simple or 1-forked, 1-1.5 mm. apart, running at ca. 70° angle; hydathodes lacking; blade glabrous to sparsely beset with minute, linear, hastate scales up to 1-2 mm. long; fertile fronds slightly shorter to somewhat longer than the sterile but otherwise nearly equal in blade size and shape; spores with broad, low, smooth ridges.

It is most easily distinguished by the obtuse blade tip and the dark, bristle-like rhizome scales. *Elaphoglossum guatemalense* may sometimes be fairly blunt-tipped but has shorter, broader rhizome scales and consistently has a more slender rhizome and with minute stellate hairs on the lower blade surface. *Elaphoglossum latifolium* has orange or brownish rhizome scales, and its blade is acuminate.

Elaphoglossum gratum (Fée) Moore, Index Fil. 10. 1857. *Acrostichum gratum* Fée, Mém. Fam. Foug. 8: 69. 1857.

Wet roadside banks, mossy cliffs, dry white clay slopes, 2,500-3,400 m.; Chimaltenango; Huehuetenango, Quezaltenango; Sacatepéquez; San Marcos; Totonicapán. Mexico (type from Veracruz, *Schaffner 279 & 322b*).

Plants terrestrial; rhizome short- to moderately creeping, to 4 mm. in diameter; rhizome scales linear-lanceolate, dark brown, lustrous, toothed, ca. 5 mm. long; phyllopodia distinct to indistinct; fronds clumped, to 20 cm. long, 1.2 cm. broad; stipe $\frac{1}{2}$ - $\frac{3}{4}$ of the frond length; stipe scales linear-lanceolate and dark-toothed or dark-tipped, spreading, 3 mm. long, some more dissected like stellate hairs and appressed; blade linear-lanceolate, apex acute to acuminate, base narrowly cuneate; veins obscure, free, simple or 1-forked, 0.6-1.0 mm. apart, running at 55-65° angle; hydathodes lacking; blade scales evenly and liberally distributed adaxially but not overlapping, linear-lanceolate, 1-1.5 mm. long, with hair teeth, on abaxial surface often reduced to resinous dots; fertile fronds generally longer than the sterile and very long-stiped (ca. $\frac{3}{4}$ of the fertile frond length), blade more acute or obtuse at apex, base more broadly cuneate; scales on abaxial midvein but not among sporangia; spores with slender, smooth crests with sparse spicules.

Elaphoglossum gratum is closely allied to *E. paleaceum*, but is smaller, longer stiped, less scaly, and terrestrial. It is somewhat like *E. pilosum*, which is also scaly, terrestrial, and of high elevation, but its scales have little body to them and the rhizome scales are tan to orange. It also resembles *E. petiolatum*, which has entire rhizome scales.

Elaphoglossum guatemalense (Kl.) Moore, Parker's Cat. 1858. *Acrostichum guatemalense* Kl., Allgem. Gartenzeitung 23: 66. 1855



FIG. 29. *Elaphoglossum*. a-b, *E. glaucum*: a, habit, fertile and sterile leaves, $\times \frac{1}{2}$; b, scales on abaxial surface, $\times 12$; c-d, *E. pilosum*: c, scales on midrib and abaxial surface, $\times 12$; d, scales on midrib and adaxial surface, $\times 12$; e-f, *E. tectum*: e, scales on midrib and abaxial surface, $\times 12$; f, scales on midrib and adaxial surface, $\times 12$; g, *E. petiolatum*, margin and glandular abaxial surface, $\times 12$; h, *E. rubescens*, scales on midrib and abaxial surface, $\times 12$.

(type from cultivation in Potsdam, Germany, grown from spores of unknown locality in Guatemala). *Acrostichum salvinii* Baker ex Hemsley, Biol. Centr. Amer. 3: 688. 1885 (type from Volcán de Fuego, Guatemala, *Godman & Salvin* 54,226).

Mostly on trees, occasionally at base of boulders, 0-2,500 m.; Alta Verapaz; Baja Verapaz; Guatemala; Izabal; Petén; Quezaltenango; El Quiché; San Marcos; Sololá; Suchitepéquez; Zacapa. Southern Mexico; British Honduras; El Salvador; Honduras.

Plants epiphytic, less commonly terrestrial; rhizome short- to moderately creeping, 2-4 mm. in diameter; rhizome scales lanceolate, lustrous brown, to 5 mm. long, entire or with a few weak, short hairs; scales sometimes deciduous, leaving a naked rhizome; phyllopodia distinct; fronds clumped to slightly spaced apart, to 60 cm. long, but usually $\frac{1}{2}$ that long, 1.5-4.0 cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length, naked or with minute, reduced, appressed scales; blade linear to linear-lanceolate, apex obtuse to acuminate, base narrowly cuneate, coriaceous; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at ca. 70° angle; hydathodes lacking; blade surfaces glabrous or with minute stellate hairs, especially on the abaxial surface; fertile fronds slightly longer than the sterile fronds, the stipe longer ($\frac{1}{2}$ - $\frac{3}{4}$ of the fertile frond length) and the blade narrower; scales lacking; spores with large, round bumps or low ridges and sparse spicules.

I have placed under this name those essentially glabrous specimens which have slender, creeping rhizomes and short, lanceolate, lustrous, brown rhizome scales. There may in fact be more than one element here, as some specimens seem especially narrow with acuminate apex, some broader with bluish green blade and acuminate apex, with the bulk of the specimens with obtuse to acute apices. Most specimens are from middle elevations except for two collections from below 200 m. in Izabal.

Elaphoglossum herminieri (Bory & Fée) Moore, Index Fil. xvi. 1857. *Acrostichum herminieri* Bory & Fée, in Fée, Mém. Fam. Foug. 2: 43, t. 11. 1845.

On trees in wet lowland forests, 0-600 m.; Alta Verapaz; Izabal; Petén. Nicaragua; Costa Rica; Panama; West Indies; Colombia; Trinidad; Venezuela.

Plants epiphytic; rhizome short-creeping, to ca. 8 mm. in diameter; rhizome scales linear, orange, lax, 15-30 mm. long, entire or rarely with irregular teeth; phyllopodia lacking; fronds clumped, to 200 cm. long, 4 cm. broad; stipe lacking; blade linear-lanceolate, apex acuminate, base narrowly cuneate, coriaceous; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at ca. 70° angle; hydathodes lacking; adaxial surface essentially glabrous, abaxial surface sparsely clothed with minute, dissected, orange scales to nearly glabrous; fertile fronds much smaller than the sterile, not seen in Guatemalan material; scales lacking; spores with large bumps or short ridges with many minute holes in the spore surface.

This is perhaps the largest of all *Elaphoglossum*, reaching over 2 m. in length, and one of the few species found at low elevation. The bluish green cast to the fronds and the long, slender, orange rhizome scales are distinctive, though not unique.

***Elaphoglossum huacsaro* (Ruiz) Christ, Monogr. Elaph. 96. 1899.** *Acrostichum huacsaro* Ruiz, Dissertac. sobre la raíz de la Ratánhia 42. 1799.

On trees in wet forests, 1,000-2,000 m. Not yet found in Guatemala. Southern Mexico; Costa Rica; Panama; West Indies; Colombia to Bolivia.

Plants epiphytic; rhizome creeping, often 5-10 cm. long, 3-5 mm. in diameter; rhizome scales lanceolate, dark, lustrous, entire, 1-2 mm. long; phyllopodia lacking; fronds clumped, to 20 cm. long, 1 cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length; stipe scales ovate, dark to pale, 1 mm. long, mostly appressed, a few spreading; blade linear, apex acute to obtuse, base narrowly cuneate; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at ca. 60° angle; hydathodes lacking; blade scales reduced to resinous dots on both surfaces, scales along blade margin ovate and entire; fertile fronds far exceeding the sterile in length, but blade narrower, stipe nearly as long as the entire sterile frond; scales lacking among the sporangia; spores with low, broad ridges with many spicules that frequently coalesce at base to form minicrests.

***Elaphoglossum lanceum* Mickel, Amer. Fern J. 69: 101. 1979.**

On tree trunks in wet forests, 2,300-2,500 m.; Quezaltenango. Southern Mexico (type from Cerro Zempoaltepetl, Oaxaca, *Mickel 4900*); El Salvador; Honduras.

Plants epiphytic; rhizome short-creeping to erect, 1 mm. in diameter; rhizome scales linear-lanceolate, reddish brown, 7 mm. long; phyllopodia lacking; fronds clumped, to 34 cm. long, 2.7 cm. broad; stipe $\frac{1}{3}$ - $\frac{2}{3}$ of the frond length; stipe scales red-brown, strongly spreading, subulate, to 6 mm. long; blade lanceolate to linear-lanceolate, apex acuminate, base cuneate, very thin, margin entire to crenulate; veins conspicuous, free, simple or 1-forked, 2-3 mm. apart, running at 35-40° angle; hydathodes evident; blade scales orange-brown, subulate, 3-5 mm. long, sparse; fertile fronds shorter than the sterile, ca. 16 cm. long, blade apex acuminate, base cuneate; blade shorter in proportion to the length of the sterile blade (e.g., 13 cm. long, 4.8 cm. broad), stipe $\frac{3}{4}$ - $\frac{4}{5}$ of fertile frond length; scales mixed with the sporangia; spores with highly perforated, lace-like crests.

This species is known only from a few collections, most of which have fronds only 12-20 cm. long and distinctly lance-shaped. A large Guatemalan specimen (*Standley 85996*) is strikingly similar to *E. buchii* C. Chr. of Hispaniola and *E. smithii* (Baker) Christ of the Lesser Antilles (which may be identical to one another), in blade form, distant veins, entire, orange, rhizome scales, the scales among the sporangia, and the sparsely scaled blade. However, ours has thinner texture, more blade scales, and spores with highly perforated crests in contrast to the unperforated crests of *E. buchii* and *E. smithii*.

Elaphoglossum latifolium (Sw.) J. Sm. London J. Bot. 1: 197. 1842. *Acrostichum latifolium* Sw., Nov. Gen. Sp. Pl. Prodr. 128. 1788.

On trees or on ground in wet forests, 300-3,000 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; Izabal; Jalapa; Petén; El Quiché; San Marcos; Santa Rosa; Zacapa. Mexico; British Honduras; El Salvador; Honduras; Nicaragua; Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Bolivia and Brazil.

Plants epiphytic or terrestrial; rhizome short-creeping, rarely moderately creeping, 4-10 mm. in diameter; rhizome scales linear-lanceolate, orange to dull tan or dirty brown, occasionally somewhat lustrous, to 8 mm. long, entire; phyllopodia distinct; fronds clumped, rarely slightly spaced, to 70 cm. long, 7 cm. broad; stipe usually $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length; glabrous or sparsely clothed with spreading, lanceolate, irregularly toothed scales; blade linear-lanceolate, apex acuminate, base cuneate to broadly cuneate, coriaceous; veins obscure, free, simple to 2-forked, ca. 1 mm. apart, running at 70-80° angle; hydathodes lacking; blade surfaces glabrous or with minute stellate black hairs on the abaxial surface; fertile fronds about equal to the sterile fronds in dimensions but sometimes slightly narrower or with longer stipe; spores with short, slender crests with many minute holes in the spore surface, or with highly perforated crests.

This represents perhaps the most difficult complex in the genus. Being glabrous, the specimens lack a great source of characters. There is much variation in size, blade shape, scale color, shape, and size, but the variation does not seem to fall into discernible patterns, so I am here lumping together all those with stout rhizomes. Names commonly applied to these specimens include *E. towarensense* (Mett.) Moore and *E. longifolium* (Jacq.) J. Smith, probably neither of which pertains to these plants. There are two distinctly different spore types seen in these plants; those with highly perforated, lacy crests seem to have more widely creeping rhizomes, whereas those with many small crests have rhizomes more compact, short-creeping to suberect, but clear distinctions cannot be made at this time.

Elaphoglossum lindenii (Bory ex Fée) Moore, Index Fil. 360. 1862. *Acrostichum lindenii* Bory ex Fée, Mém. Fam. Foug. 2: 48, t. 18, f. 3. 1845 (type from Orizaba, Veracruz, *Galeotti 6263*). *A. pumilum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 23, t. 2, f. 2. 1842 (type from Orizaba, *Galeotti 6263*: based on same collection as *A. lindenii*, but from different herbarium), not *E. pumilum* Lam & Verhey ex H. J. Lam, 1945. *A. venustum* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 168 (seors. 16). 1849 (type from Orizaba, Veracruz, Mexico, *Liebmann 2420*), not *A. venustum* Fée, 1857. *E. liebmanni* Moore, Index Fil. 360. 1862, based on *A. venustum* Liebm.

On wet banks and rocky cliffs, rarely on tree trunks, 2,700-3,500 m.; Quezaltenango; Sacatepéquez; San Marcos; Totonicapán. Mexico; Costa Rica; Panama; Colombia, south to Chile.

Plants terrestrial or epipetric, rarely epiphytic; rhizome short-creeping, ca. 3 mm. in diameter; rhizome scales linear, maroon, to 8 mm. long, with short teeth; phyllopodia lacking; fronds clumped, to 40 cm. long, but generally much shorter, 4 cm. broad; stipe $\frac{1}{2}$ - $\frac{3}{4}$ of the frond length; stipe scales orange to maroon, subulate, widely spreading, 2-3 mm. long; stipe also with a few minute erect glandular hairs; blade ovate to ovate-lanceolate, apex cuspidate, base rounded or subcordate; veins evident, free, simple or 1-forked, ca. 2 mm. apart, running at 60-70° angle; hydathodes distinct; blade scales subulate, orange to maroon, abundant on abaxial surface, few adaxially, especially spreading from the margin, 2-3 mm. long; fertile fronds slightly shorter than the sterile, the blade more elliptic, to 4.2 cm. long, 2.4 cm. broad, stipe to $\frac{4}{5}$ of the fertile frond length; apex obtuse, blade often folded at the midvein; scales on the abaxial midvein but not among the sporangia; spores with low crests and many holes in the spore surface.

The plants are usually small but the species is highly variable. It is distinguished by the blade shape, the generally cuspidate blade apex, and the folded fertile blade. It may be mistaken for a small specimen of *E. crinipes* but the latter has lighter colored blade scales, acuminate blade apex, and the spores are echinate.

Elaphoglossum mathewsii (Fée) Moore, Index Fil. 12. 1857. *Acrostichum mathewsii* Fée, Mém. Fam. Foug. 2: 54, t. 2, f. 2. 1845. *A. hartwegii* Fée, Mém. Fam. Foug. 2: 53, t. 9, f. 2. 1845. *E. hartwegii* (Fée) Moore, Index Fil. xvi. 1857. *A. pringlei* Davenp., Bot. Gaz. 21: 253. 1894 (type from Cerro San Felipe, Oaxaca, Mexico, *Pringle 5605*). *E. pringlei* (Davenp.) C. Chr., Index Fil. 313. 1905.

On rocks in pine forests, 3,000-3,800 m.; Chimaltenango; Huehuetenango; Sacatepéquez; San Marcos; Totonicapán. Southern Mexico; Colombia and Venezuela, south to Chile.

Plants epipetric; rhizome long-creeping, 1-1.5 mm. in diameter; rhizome scales linear-lanceolate, castaneous, lustrous with markedly paler margins, with sagittate base, entire, ca. 3 mm. long; phyllopodia distinct; fronds spaced, often 1 cm. apart, to 22 cm. long, 1.2 cm. broad; stipe $\frac{1}{2}$ - $\frac{3}{4}$ of the frond length; stipe scales mostly 1-2 mm. long, brown with pale margin, appressed to slightly spreading, entire to slightly toothed; blade linear-lanceolate, apex acuminate to acute or obtuse, base cuneate; veins inconspicuous, free, simple or 1-forked, 0.8-1 mm. apart, running at 60-70° angle; hydathodes present but inconspicuous; blade scales of abaxial surface generally abundant but not overlapping, lanceolate to deltoid, peltate, brown with pale margins, adaxial surface often essentially glabrous; fertile fronds slightly taller than the sterile, longer stipe ($\frac{3}{5}$ - $\frac{4}{5}$ of the fertile frond length); scales sparse on abaxial midvein, lacking among the sporangia; spores with low, broad ridges and abundant spicules covering all surfaces.

Most likely *E. hartwegii* and *E. mathewsii* are the same. Fée described them at the same time and carefully distinguished them, *E.*



FIG. 30. *Elaphoglossum*. a-b, *E. paleaceum*: a, habit, fertile and sterile leaves, $\times \frac{1}{2}$; b, scales on abaxial surface (darker ones along midrib), $\times 12$; c, *E. auricomum*, scales on abaxial surface, $\times 12$; d, *E. muscosum*, scales on abaxial surface, $\times 12$; e, *E. mathewsii*, scales on abaxial surface, $\times 12$.

hartwegii having entire scales on both the blade and the rhizome, *E. mathewsii* having ciliate laminar scales and slightly toothed rhizome scales. The former is terrestrial, the latter supposedly epiphytic; the former with upper blade surface glabrous, the latter scaly; the former with fertile fronds longer than the sterile, the latter with fertile and sterile about the same length. These differences, however, do not seem to hold true. Specimens in Mexico and Guatemala tend to be somewhat broader than those of South America, but more intensive studies are necessary in this complex before distinctions can be made with confidence.

***Elaphoglossum muscosum* (Sw.) Moore**, Index Fil. 12. 1857. *Acrostichum muscosum* Sw., Prodr. 128. 1788. *E. hookerianum* Underw. ex Maxon, Contr. U.S. Natl. Herb. 13: 6. 1909 (type from Coban, Alta Verapaz, Guatemala, *Tuerckheim II*. 1862).

On trees in wet forests, 1,400-3,200 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Totonicapán; Zacapa. Southern Mexico; El Salvador; Honduras; Costa Rica; Panama; West Indies; Colombia.

Plants epiphytic; rhizome short-creeping to erect, to 12 mm. in diameter; rhizome scales linear, reddish orange, to 13 mm. long, with short teeth; phyllopodia inconspicuous or lacking; fronds clumped, to 30 cm. long, 4.8 cm. broad; stipe $\frac{2}{5}$ - $\frac{3}{5}$ of the frond length; stipe scales large, light orange, with many small teeth, to 6 mm. long, spreading; blade narrowly elliptic, or ovate-lanceolate, apex obtuse, base broadly cuneate to rounded, subcoriaceous; veins inconspicuous, free, simple or 1-forked, ca. 1 mm. apart, running at ca. 60° angle; hydathodes lacking; blade scales of adaxial surface white, or with slightly darker centers, peltate, ovate-lanceolate, long-toothed, abundant; on abaxial surface longer, darker orange, less peltate; fertile fronds as long as the sterile fronds, but smaller blade and longer stipe (ca. $\frac{1}{2}$ of the fertile frond length); scales sparse, small, and inconspicuous among the sporangia; spores sparsely covered with short tubercles.

Elaphoglossum muscosum belongs to a very distinct group with few species that are distinguished by the blade shape, the densely clothed stipe, and the spore morphology. This species is distinguished from *E. engelii* by the inconspicuous scales among the sporangia, the less toothed scales, and the rhizome habit.

***Elaphoglossum paleaceum* (Hook. & Grev.) Sledge**, Bull. Brit. Mus. (Nat. Hist.) Bot. 4 (2): 95. 1967. *Acrostichum paleaceum* Hook. & Grev., Icon. Fil. 2: t. 235, Alph. Index et Syst. Index. 1831. *A. squamosum* Sw., J. Bot. (Schrader) 1800²: 11. 1801 [1802] (not Cavanilles, 1799). *E. squamosum* (Sw.) J. Sm. J. Bot. (Hooker) 4: 148. 1841. *E. hirtum* (Sw.) C. Chr., Index Fil. 308. 1905, *sensu auctt.*, not *A. hirtum* Sw., J. Bot. (Schrader) 1800²: 10. 1801 [1802].

On trees or rocks in wet forests, 1,800-3,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Esquintla; Guatemala; Huehuetenango; El Progreso; El Quiché; San Marcos; Sololá; Totonicapán. Mexico; El Salvador; Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Bolivia and Brazil; Azores and Madeira.

Plants epiphytic or epipetric; rhizome short-creeping, to 10 mm. in diameter; rhizome scales linear-lanceolate, brown to black and opaque, ca. 5 mm. long, margin with long, hairlike teeth; phyllopodia distinct; fronds clumped, to 53 cm. long, often 2 (to 3.5) cm. broad; stipe $\frac{1}{4}$ - $\frac{1}{2}$ of the frond length, densely clothed with spreading, black or orange scales, similar to those of the rhizome, to 3 mm. long; blade linear to linear-lanceolate, apex acuminate, base broadly cuneate to rounded; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at ca. 70° angle; hydathodes lacking; blade scales abundant, overlapping, lanceolate, ca. 2 mm. long, long hair-toothed, usually those of the stipe and midvein dark, dark ones sometimes scattered in lower part of the blade; fertile fronds shorter than the sterile, to 28 cm. long, 1.4 cm. broad, but with same shape; scales along the abaxial midvein and only occasionally among the sporangia; spores with low, broad, smooth ridges.

There is considerable variation in scale coloration, ranging from many black scales to none. This species has until recently gone under the name *E. hirtum* (Sw.) C. Chr., but Swartz's original plant was found to be *E. undulatum* of the Lesser Antilles and Costa Rica. *Elaphoglossum paleaceum* is part of a pantropic complex that requires considerable attention to clarify the taxonomic confusion.

Elaphoglossum petiolatum (Sw.) Urban, Symb. Antill. 4: 61. 1903. *Acrostichum petiolatum* Sw. Nov. Gen. Sp. Pl. Prodr. 128. 1788. *A. viscosum* Sw., Syn. Fil. 10, 193. 1806. *E. viscosum* (Sw.) J. Sm. J. Bot. (Lond.) 4: 148. 1841. *A. schiedei* Kunze, Anal. 10. 1837 (type from Jalapa, Veracruz, Mexico, *Schiede s.n.*). *A. schmitzii* Mett. ex Kuhn, Linnaea 36: 51. 1869 (type from locality unknown, Mexico, *Schmitz 3 pp.*).

On trees or shaded banks, 1,600-3,150 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Huehuetenango; Quezaltenango; El Quiché; San Marcos; Totonicapán. Mexico; Honduras; Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Peru and Brazil; Old World tropics.

Plants epiphytic or terrestrial; rhizome short-creeping, 3-5 mm. in diameter; rhizome scales linear, blackish maroon to castaneous with kinky hair tip, ca. 3 mm. long, entire; phyllopodia distinct but very short (2-3 mm. long); fronds clumped, to 39 cm. long, 3.4 cm. broad; stipe ca. $\frac{1}{4}$ of the frond length, clothed with scales 1-2 mm. long, some spreading and broader, some narrow and appressed, entire or toothed to stellate; blade linear-lanceolate, apex acuminate, base cuneate; veins visible, free, simple or 1-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales sparse, linear-lanceolate with hair teeth, mostly on the adaxial surface and on young fronds, often more abundant near the margins; abaxial surface scales reduced to resinous dots

mixed with stellate hairs, or less commonly with only stellate hairs or scales as on adaxial surface, rarely glabrous; fertile fronds about same length as the sterile fronds but longer stipe, ca. $\frac{2}{3}$ of the frond length; scales on the abaxial midvein; spores with broad, low, smooth ridges.

There is considerable variation in the degree of resinous dotting and scaliness, especially on the abaxial surface, but the significance of this variation is not yet understood. *Elaphoglossum petiolatum* closely resembles *E. huacsaro* in the resinous dots of the abaxial blade surface and the frequent concentration of scales along the margin, but *E. huacsaro* has a more erect rhizome, an obtuse blade apex, and the fertile frond longer than the sterile.

Elaphoglossum piloselloides (Presl) Moore, Index Fil. 13. 1857. *Acrostichum piloselloides* Presl, Rel. Haenk. 1: 14, t. 2, f. 1. 1825.

On moist shaded banks and rocks, rarely reported on trees, 1,600-2,800 m.; Alta Verapaz; Chimaltenango; Escuintla; El Quiché; Sacatepéquez; Sololá; Totonicapán. Mexico; El Salvador; Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Chile.

Plants terrestrial or epipetric, rarely epiphytic; rhizome short-creeping to suberect, ca. 2 mm. in diameter; rhizome scales linear, orange, entire, 3-6 mm. long; phyllopodia lacking; fronds clumped, to 8 (often only 2-4) cm. tall, 1 cm. broad; stipe slender, usually $\frac{3}{4}$ - $\frac{1}{2}$ of the frond length, moderately clothed with tan to orange, very narrow, subulate scales, 2-4 mm. long; blade spatulate, ovate-lanceolate to narrowly elliptic, apex obtuse, base broadly cuneate; veins obscure, free, simple, or rarely 1-forked, ca. 1 mm. apart, running at ca. 40-50° angle; hydathodes present but inconspicuous; blade scales somewhat subulate (slightly rolled at base), tan to dull orange, uniformly and moderately covering the blade surfaces; fertile fronds as tall as or taller than the sterile, more erect, stipe ca. $\frac{1}{2}$ of the fertile frond length, blade smaller than the sterile, often folded in half, spatulate to nearly round; scales of blade and upper stipe dark brown to black, shining, scale bases not inrolled but spreading and slightly toothed; soral scales absent except for base of midvein; spores with smooth, broad, low ridges.

This differs slightly from *E. spatulatum* (Bory) Moore of Bourbon Island and Africa and often is placed under that name. Further study may show them to be the same, however.

Elaphoglossum pilosum (Humb. & Bonpl. ex Willd.) Moore, Index Fil. 13. 1857. *Acrostichum pilosum* Humb. & Bonpl. ex Willd., Sp. Pl. 5: 103. 1810. *A. venustum* Fée, Mém. Fam. Foug. 8: 68. 1857 (type from Mecameca, Puebla, Mexico, *Schaffner 322b,c*), not Liebm. 1849. *E. venustum* (Fée) Moore, Index Fil. 16. 1857. *A. mulleri* Fourn., Mex. Pl. 1: 68, t. 1, f. 2. 1872 (type from Ulnapa, Veracruz, Mexico, Müller 41 *quinter*). *A. araneosum* D.C. Eat., Proc. Amer. Acad. 22: 461. 1887 (type from Río Blanco, Jalisco, Mexico, *Palmer 333*). *E. araneosum* (D.C. Eat.) C. Chr., Index Fil. 303. 1905. *E. mulleri* (Fourn.) C. Chr., *tom. cit.* 311.



FIG. 31. *Elaphoglossum*. a-b, *E. crinipes*: a, habit, rhizome with fertile and sterile leaves, $\times \frac{1}{2}$; b, leaf margin with scales and hydathodes, $\times 6$; c, *E. erinaceum*, scales of leaf margin, $\times 6$; d-e, *E. piloselloides*: d, habit, rhizome with fertile and sterile leaves, $\times \frac{1}{2}$; e, scales on abaxial surface, $\times 6$; f-g, *E. squamipes*: f, habit, creeping rhizome with fertile and sterile leaves, $\times \frac{1}{2}$; g, scales on abaxial surface, $\times 6$.

On banks, moist shaded slopes, or on rocks, 1,500-2,100 m.; Baja Verapaz; Chiquimula; Guatemala; Huehuetenango; Santa Rosa. Mexico; Costa Rica; Colombia and Venezuela.

Plants terrestrial or epipetric; rhizome short-creeping, to 5 mm. in diameter; rhizome scales orange, ovate-lanceolate to nearly deltoid, ca. 2 mm. long, entire or weakly toothed; phyllopodia lacking; fronds clumped, to 33 cm. long, 2.5 cm. broad; stipe $\frac{1}{5}$ - $\frac{1}{2}$ of the frond length, clothed with orange scales; scales few, linear-lanceolate, more as stellate hairs, somewhat deciduous with age; blade linear-lanceolate, apex acuminate, base narrowly cuneate, thin; veins visible but not conspicuous, free, simple to 2-forked, 0.4-0.7 mm. apart, running at ca. 70° angle; hydathodes lacking; blade scales as stellate hairs on both adaxial and abaxial surfaces with virtually no scale body at all, ca. 1 mm. long, occasionally with a few linear-lanceolate scales on the abaxial midvein; fertile frond about the same length as the sterile but longer stipe (nearly $\frac{1}{2}$ of the fertile frond length) and narrower blade (to 0.8 cm. broad); stellate scales on abaxial midvein but lacking among sporangia; spores with smooth, low, slender crests.

This species is quite variable in degree of scaliness and size of plants. It can be distinguished from *E. petiolatum*, *E. gratum*, and *E. stellatum* by its orange rhizome scales. It is most abundant in Mexico and very rare south of Guatemala. The type is from Venezuela, and if that turns out to be a different species, then the correct name for the Mexican-Guatemalan material would be *E. venustum* (Fée) Moore.

Elaphoglossum revolutum (Liebm.) Moore, Index Fil. 365. 1862. *Acrostichum revolutum* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 163 (seors. 11). 1849. *A. rampans* Baker, Syn. Fil. 518. 1874. *E. rampans* (Baker) Christ, Monogr. Elaph. 56. 1899.

On tree trunks in wet forests, 300-800 m.; Alta Verapaz; Huehuetenango; Petén. Southern Mexico (type from Chinantla, Oaxaca, Mexico, *Liebmann 2427*); Costa Rica; Panama; West Indies; Colombia.

Plants epiphytic; rhizome long-creeping, ca. 1 mm. in diameter; rhizome scales ovate-lanceolate, orange, ca. 3 mm. long, entire; phyllopodia lacking; fronds spaced usually 4-8 mm. apart, to 8.5 cm. long, 1.1 cm. broad; stipe ca. $\frac{1}{4}$ (to $\frac{1}{2}$) of the frond length, clothed with orange, ovate, somewhat spreading scales, 2 mm. long; blade narrowly elliptic, apex obtuse, base cuneate; coriaceous; veins obscure, free, simple or 1-forked, ca. 0.8 mm. apart, running at ca. 60° angle; hydathodes lacking; blade glabrous or with a few ovate scales on the abaxial midvein; fertile fronds about same length as the sterile fronds, stipe $\frac{1}{2}$ - $\frac{3}{4}$ of the fertile frond length; blade narrow, to 4 mm. wide; scales lacking on the abaxial surface; spores with low, broad ridges, with abundant spicules on all surfaces.

Closely allied to *E. squamipes* and to *Peltapteris*, as evidenced by the rhizome habit, the scales, and the spores. It is distinguished from *E. affine* and small specimens of *E. guatemalense* by the pale, ovate, rhizome scales and the lack of phyllopodia.

Elaphoglossum rigidum (Aubl.) Urban, Symb. Antill. 9: 374. 1925. *Polypodium rigidum* Aubl., Hist. Pl. Guian. 2: 963. 1775. *Acros-*

tichum flaccidum Fée, Mém. Fam. Foug. 2: 35, t. 7, f. 2. 1845. *E. flaccidum* (Fée) Moore, Index Fil. 356. 1862.

On trees in wet forests, 65-500 m.; Alta Verapaz; Izabal. Southern Mexico; British Honduras; Nicaragua; Costa Rica; Panama; West Indies; Colombia, Venezuela.

Plants epiphytic; rhizome short-creeping, ca. 3 mm. in diameter; rhizome scales brown, thin, linear-lanceolate, entire, to 6 mm. long; phyllopodia distinct; fronds clumped, to 25 cm. tall, 3.2 cm. broad; stipe short to nearly lacking, to $\frac{1}{4}$ of the frond length, clothed with a few strongly toothed scales, ca. 2 mm. long; blade oblanceolate, apex acuminate, base narrowly cuneate, decurrent; veins inconspicuous, free, simple or 1-forked, ca. 1 mm. apart, running at 70-80° angle; hydathodes lacking; blade scales many to few minute stellate hairs on abaxial surface, lacking on adaxial surface; fertile fronds about equal in length to the sterile fronds or somewhat shorter with the stipe being nearly $\frac{1}{2}$ the fertile frond length; scales lacking on the abaxial surface; spores with many small crests and with minute holes in the spore surface.

Elaphoglossum rubescens Christ, Monogr. Elaph. 93, f. 47-48. 1899.

On tree trunks in wet forests, 600-1,600 m.; Alta Verapaz (type without specific locality, *Bernoulli* 320). Southern Mexico.

Plants epiphytic; rhizome short-creeping, ca. 5 mm. in diameter; rhizome scales castaneous, lustrous, linear-lanceolate, 4 mm. long, entire or with short, weak teeth; phyllopodia distinct; fronds clumped, to 45 cm. long, 3.2 cm. broad; stipe ca. $\frac{1}{4}$ of the frond length, stout; stipe sparsely clothed with linear-lanceolate, spreading, lustrous, castaneous scales to 1 mm. long; stipe more copiously covered with small, appressed, tan scales which are shorter, with long hair-teeth, reduced nearly to stellate hairs; blade linear, apex caudate, base broadly cuneate, papyraceous; veins obscure, free, simple or 1-forked, 1-1.2 mm. apart, running at 70° angle; hydathodes lacking; blade scales abundant but not overlapping, adaxial surface scales delicate, white, appressed, subdeltoid, with short hair-teeth or scales lacking with age; abaxial surface scales orange, narrow to deltoid, with long hair-teeth, distinctly upturned margins; blade margin especially scaly with scales flat and overlapping; fertile fronds about equal to the sterile fronds in length but narrower blade (0.7-0.9 cm. wide) and longer stipe (ca. $\frac{1}{2}$ of the fertile frond length), scales on midvein of abaxial surface but not among the sporangia; spores with sparse, low, slender ridges and low protuberances in areas between the ridges.

This species is distinct in its linear blade, caudate tip, and upturned blade scale margins. It is allied to *E. paleaceum* in the hairlike teeth of the blade scales, but the rhizome scales are not as long-toothed. It also closely resembles *E. auricomum* but has a longer stipe and shorter scale hairs on the blade and rhizome.

Elaphoglossum setosum (Liebm.) Moore, Index Fil. 366. 1857. *Acrostichum setosum* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 169 (seors. 17). 1849, not Wall, 1828 (*nom. nud.*). *A. recognitum* Fourn., Mex. Pl. 1: 67. 1872 (renaming of *A. setosum*

Liebm.). *E. catherinae* Underw. ex Maxon, Contr. U.S. Natl. Herb. 13: 5. 1909 (type from Pansamalá, Alta Verapaz, Guatemala, *Tuerckheim* [J. Donnell-Smith 1003]).

On tree trunks of wet forests, 800-1,400 m.; Alta Verapaz. Mexico (type from Huitamalco, Veracruz, *Liebm. 2433*); Costa Rica.

Plants epiphytic; rhizome short-creeping, 1-2 mm. in diameter; rhizome scales linear, with sparse and irregular short teeth, brown to dull orange, 3-5 mm. long; phyllopodia lacking; fronds clumped, spreading to somewhat pendent, to 18 cm. long, 1.5 cm. broad; stipe slender, $\frac{1}{5}$ - $\frac{2}{5}$ of the frond length, moderately clothed with slender, dull-orange, subulate spreading scales, 2-3 mm. long; blade linear-lanceolate, apex gradually acuminate, base cuneate, thin; veins conspicuous, free, mostly simple or rarely 1-forked, 1.5-2 mm. apart, running at ca. 40° angle; hydathodes conspicuous; blade scales subulate, dull orange, moderately and uniformly clothing the blade surface, more so on the abaxial surface, longer and spreading at the margin; fertile fronds nearly as long as the sterile but more elliptic with acute apex, ca. 3 cm. long and 1.1 cm. broad, and longer stiped (ca. $\frac{3}{4}$ of the fertile frond length), with abundant scales mixed with the sporangia; spores with many narrow, highly perforated crests.

Superficially much like *E. crinipes*, but it can be distinguished by the smaller size, the presence of scales among the sporangia, and quite different spores. It is also like *E. lindenii*, which has more elliptic blades and darker blade scales.

Elaphoglossum siliquoides (Jenm.) C. Chr. Index Fil. 315. 1905.
Acrostichum siliquoides Jenm. J. Bot. 19 (N.S. 10): 53. 1881.

On tree trunks in wet forests, 800-1,200 m.; Alta Verapaz. Costa Rica; Panama; West Indies.

Plants epiphytic; rhizome short-creeping, ca. 8 mm. in diameter; rhizome scales linear, entire, orange, ca. 5 mm. long; phyllopodia lacking; fronds clumped, to 45 cm. long, 2.5 cm. broad; stipe ca. $\frac{1}{3}$ of the frond length, clothed with many, long, reddish, subulate scales, often to 13 mm. long; stipe also with minute, erect, glandular hairs; blade broadly linear, tapering gradually at both ends, thin; veins obscure, free, simple or 1-forked, 1.5-2 mm. apart, running at ca. 50° angle; hydathodes present but inconspicuous; blade scales subulate, reddish, extremely long and conspicuous (to 10 mm. long), uniformly and liberally distributed over the surfaces and margin and midvein; blade also with minute, erect, glandular hairs; fertile fronds ca. $\frac{1}{2}$ as long as the sterile, to 15 cm. long, stipe ca. $\frac{3}{4}$ of the fertile frond length, blade spatulate to ovate-lanceolate, apex obtuse, base slightly cuneate, sterile margin ca. 1 mm. wide; scales on the stipe and adaxial fertile blade surface, lacking on the abaxial blade surface; spores with short, low, broad, smooth ridges and holes in the spore surface.

A very distinct species in its linear frond with extremely long, subulate blade scales. It is probably most closely allied to *E. apodum* in its subulate scales, vein angles, no hydathodes, glandular hairs, and similar spores. *Johnson 290* label reports "leaves give pleasant odor when bruised." To my knowledge this has not been reported for other *Elaphoglossum* species.

Elaphoglossum squamipes (Hooker) Moore, Index, Fil. 15. 1857. *Acrostichum squamipes* Hooker, Icon. Pl. t. 197. 1837. *A. ovatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 164 (seors. 12). 1849 (type from Cerro Zempoaltepetl, Oaxaca, Mexico, Liebmann 2431), not Hooker and Greville, 1829. *E. subaequale* Moore, Index Fil. 368. 1862, based on *A. ovatum* Liebm.

On trees in wet oak forest, ca. 3000 m.; Chimaltenango; Huehuetenango. Mexico; Costa Rica; Panama; Colombia and Venezuela, south to Bolivia and Brazil.

Plants epiphytic; rhizome long-creeping, ca. 1 mm. in diameter; rhizome scales ovate to linear-lanceolate, dull orange, peltate, entire, 3-6 mm. long; phyllopodia lacking; fronds distant, erect to spreading, to 8 cm. long, 1.5 cm. broad; stipe slender, ca. $\frac{1}{2}$ of the frond length, moderately clothed with ovate, dull-orange scales, 2-3 mm. long; blade spatulate, apex obtuse, base broadly cuneate; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales sparse, small, inconspicuous, 1-2 mm. long, linear, often coarsely and irregularly toothed, especially toward the scale base, more frequent on the abaxial surface; fertile fronds as tall as or slightly taller than the sterile fronds, with longer stipe, ca. $\frac{3}{4}$ of the fertile frond length, blade spatulate, smaller than the sterile with a few scales along the abaxial midvein but lacking among the sporangia; spores with broad, low ridges and abundant spicules covering all surfaces.

Elaphoglossum squamipes represents a distinct group with long-creeping rhizomes and broad, pale rhizome and stipe scales. It is very closely related to *Peltapteris*, which could justifiably be placed in *Elaphoglossum*, differing from *E. squamipes* et aff. only in frond architecture.

Elaphoglossum stellatum Mickel, Amer. Fern J. 69: 101. 1979.

On soft cliffs and clay banks, or epiphytic, 2,000-2,500 m.; Alta Verapaz; Quezaltenango; Santa Rosa (type from Volcán Tecuamburro, Steyermark 33155).

Plants terrestrial, epipetric, or epiphytic; rhizome short-creeping, ca. 2 mm. in diameter; rhizome scales linear-lanceolate, castaneous, ca. 2 mm. long, entire; phyllopodia distinct; fronds clumped, to 20 cm. long, 0.9 cm. broad; stipe ca. $\frac{1}{4}$ of the frond length, sparsely clothed with stellate hairs; blade linear, apex acuminate, base cuneate; veins barely visible, free, simple or 1-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; scales sparse, stellate hairs on the abaxial surface, especially on the midvein, those on the adaxial surface with slight scale body; fertile fronds shorter and narrower and longer stiped than the sterile, to 10 cm. long, 0.5 cm. wide, stipe ca. $\frac{1}{2}$ of the fertile frond length; stellate hairs on abaxial midvein but not among the sporangia; spores with low ridges.

This is distinguished from *E. petiolatum* by the lack of glandular dots on the abaxial surface and lack of broader scales on the adaxial surface and stipe, and the lighter rhizome scale color. It is distin-

guished from *E. pilosum* by the darker rhizome scales, small blade size, and narrow blade. *Steyermark 35012* and *33155* are much smaller but have the same castaneous rhizome scales and stellate hairs on both blade surfaces.

Elaphoglossum tambillense (Hooker) Moore, Index Fil. 15. 1857. *Acrostichum tambillense* Hooker, Icon. Pl. t. 656. 1844. *A. pallidum* Baker ex Jenm. J. Bot. 17 (N.S. 8): 263. 1879. *E. pallidum* (Baker ex Jenm.) C. Chr. Index Fil. 312. 1905.

Wet shaded banks or rocks, less commonly on trees, 2,300-3,300 m.; Chimaltenango; Quezaltenango; San Marcos; Sololá. Southern Mexico; Costa Rica; Panama; Jamaica; Hispaniola; Colombia to Ecuador.

Plants terrestrial, epipetric, or epiphytic; rhizome short-creeping, to 8 mm. in diameter; rhizome scales brown to maroon, stiff, to 12 mm. long; phyllopodia lacking; fronds clumped, to 50 cm. long, 6 cm. broad; stipe $\frac{1}{3}$ - $\frac{1}{2}$ of the frond length; stipe scales subulate, spreading, sparse or lacking; stipe also with a few minute, erect, glandular hairs; blade narrowly lanceolate, apex caudate, base cuneate to rounded, papyraceous; veins evident, free, 1- or 2-forked, 1.5-2 mm. apart, running at 70-80° angle; hydathodes lacking; blade scales black, subulate, generally early deciduous, mostly along the margin, mature specimens with only a few or totally lacking; blade also with minute, black, stellate hairs; fertile fronds much smaller than the sterile; scales lacking among the sporangia; spores with low, narrow ridges and with holes in the spore surface.

Closely allied to *E. albomarginatum*; see discussion under that species.

Elaphoglossum tectum (Humb. & Bonpl. ex Willd.) Moore, Index Fil. 15. 1857. *Acrostichum tectum* Humb. & Bonpl. ex Willd. Sp. Pl. 5: 102. 1810. *A. rubiginosum* Fée, Mém. Fam. Foug. 2: 47, t. 5, f. 1; t. 13, f. 1. 1845.

Generally on wet shaded banks or rocky slopes, less commonly on tree trunks in wet forests, 1,750-2,500 m.; Alta Verapaz; Guatemala; Huehuetenango; El Quiché; Sacatepéquez. Mexico; Costa Rica; Panama; West Indies; Colombia and Venezuela, south to Bolivia and Brazil.

Plants terrestrial, epipetric, less commonly epiphytic; rhizome short- to moderately creeping, 2-3 mm. in diameter; rhizome scales linear-lanceolate, dark reddish black, sclerotic, lustrous, ca. 5 mm. long, with a few pale, weak hair-teeth; phyllopodia indistinct; fronds clumped to slightly spaced, to 3 mm. apart, to 80 cm. long, 3 cm. broad; stipe $\frac{1}{3}$ - $\frac{1}{2}$ the frond length; stipe scales appressed, peltate, round with dark center and short hair-teeth; blade linear, apex long-acuminate, base narrowly cuneate; veins obscure, free, simple or 1-forked, mostly 0.7-1 mm. apart, running at ca. 80° angle; hydathodes lacking; blade scales on adaxial surface to glabrous with age, white appressed, round, peltate, toothed, on the abaxial surface reduced to stellate hairs; fertile fronds about as long as the sterile or slightly longer but narrower blade and longer stipe (more than $\frac{1}{2}$ of the fertile frond length); scales round, peltate on abaxial midvein but lacking among the sporangia; spores with broad, low, smooth ridges.

This species is readily distinguished by the round, peltate scales on the stipe and adaxial surface.

Elaphoglossum tenuifolium (Liebm.) Moore, Index Fil. 368. 1862. *Acrostichum tenuifolium* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 11. 1849 (type from Mexico, Oaxaca, Cerro Zempoaltepetl, *Liebmann 2654*).

On rocks, 2,400-3,000 m.; Quezaltenango. Mexico.

Plants terrestrial or epipetric; rhizome short to moderately creeping, 1-2 mm. in diameter; rhizome scales dense to sparse, ovate, orange or tan with varying degrees of dark, shiny, sclerotic streaking, ca. 3 mm. long, deeply cordate, appearing nearly peltate, entire or with occasional small, irregular teeth; phyllopodia distinct; fronds spaced 1-8 mm. apart, 6-23 cm. long, 0.6-1.0 cm. broad; stipe $\frac{1}{4}$ - $\frac{2}{3}$ of the frond length, glabrous or with tan, ovate scales; blade linear-elliptic, apex acuminate, base attenuate; veins obscure, free, simple or 1-forked, ca. 1 mm. apart, running at 60-70° angle; hydathodes lacking; blade scales sparse, minute stellate hairs or dots on abaxial surface, rare on adaxial surface; fertile fronds similar to the sterile in size and shape or occasionally slightly longer; scales lacking on abaxial surface; spores with low ridges or small narrow crests.

See comments under *E. affine*.

ERIOSORUS Fée

REFERENCE: A. F. Tryon, A monograph of the fern genus *Eriosorus*, Contr. Gray Herb. 200: 54-174. 1970.

Plants terrestrial; rhizome creeping or decumbent, densely provided with trichomes or terete, rigid bristles (in one variety with a few scales); leaves densely crowded, determinate or indeterminate, erect to scandent, 0.4-4 m. long, essentially monomorphic (though in a few species, the fertile segments somewhat constricted); petiole not articulate, terete or subterete, castaneous to atropurpureous, commonly lustrous, pubescent or glabrate; lamina linear to narrowly triangular, 10-50 cm. broad, (1) 2- to 5- (6-) pinnate, firm-herbaceous to subcoriaceous, glabrous (adaxially) to densely pubescent or glandular; rachis atropurpureous to castaneous to (rarely) light brown, sulcate adaxially, in some species slightly to strongly flexuous; pinnae spreading to ascending or (occasionally) descending, deltoid-lanceolate to -ovate, the costae (in a few species) sometimes flexuous; ultimate segments ovate to obovate or orbicular or narrow-elliptic, often bifid, the margins plane to revolute, undifferentiated, or slightly to prominently thickened into a yellowish, continuous rim; veins free, dichotomous, terminating at the margin or obviously short of it, the tips slightly thickened to clavate (especially as seen from the adaxial side); sporangia short-stalked, not arranged in discrete sori, borne abaxially along the veins, at maturity sometimes nearly spreading across the narrow segments; indusia lacking; spores trilete, tetrahedral, and usually provided with a rather broad, equatorial ridge, with perine.

Of Guatemalan genera, *Eriosorus* is most closely related to *Anogramma*, *Jamesonia*, and *Pityrogramma*, but can hardly be confused with either. Its species lack the ceraceous indument and rhizome scales of *Pityrogramma*. *Anogramma* is at least sparsely scaly on the

rhizome, and the leaves are smaller and much more delicate than those of *Eriosorus*. *Jamesonia* lacks scales, as in *Eriosorus*, but its strict habit and simple, orbicular, imbricate pinnae render it clearly distinct.

The 25 species of *Eriosorus* are confined to the neotropics, with the greatest representation in Brazil and the Andes. The taxonomy is frequently confused by the tendency of a number of species to hybridize, and by the fact that collections are often incomplete (e.g., lacking rhizomes). In Guatemala are found the typical varieties of three species.

- a. Lamina 4- to 5-pinnate, glabrous to sparsely pubescent; leaves to 3 m. long, larger ones scandent; rachis (and often costae) strongly flexuous. *E. flexuosus*.
- a. Lamina 2-pinnate to nearly 3-pinnate-pinnatisect, moderately to densely pubescent (at least abaxially); leaves less than 1 m. long, erect; rachis and costae straight to slightly flexuous.
 - b. Veins terminating at or very near the segment margin; margin not or weakly differentiated, the rim, if any, thin and inconspicuous. *E. hirtus*.
 - b. Veins terminating well short of the segment margin; margin strongly differentiated, with a continuous, conspicuous, yellow, subcartilaginous rim. *E. hispidulus*.

Eriosorus flexuosus (HBK) Copel. Gen. Fil. 58. 1947. *Gymnogramma flexuosus* Desv., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 306. 1811 (Desvaux's epithet not transferable to *Eriosorus*). *Grammitis flexuosa* HBK, Nov. Gen. et Sp. 1: 5. 1816 (not HB, 1809). *Gymnogramma refracta* Kunze ex Kl., Linnaea 20: 410. 1847. *Psilogramme flexuosa* (HBK) Kuhn, Fests. 50 Jubil. Reals. Berlin: Chaetop. 339. 1882. *P. refracta* (Kunze ex Kl.) Maxon, Bull. Torrey Bot. Club 42: 84. 1915. *P. villosula* Maxon, *tom. cit.* 83. *Gymnogramma villosula* (Maxon) C. Chr. Index Fil. Suppl. Prelim. 19. 1917. *E. villosulus* (Maxon) Scamman, Contr. Gray Herb. 191: 88. 1962.

In forests, thickets, and shaded ravines, sometimes on partly open slopes or banks, often scandent on surrounding vegetation, 2,200-3,000 m.; Huehuetenango; El Progreso; Zacapa. Southern Mexico to Panama; Hispaniola; Colombia to British Guiana, south to Bolivia and Brazil.

Rhizome slender, provided with stout, terete, appressed, bristle-like trichomes, these lustrous, castaneous to blackish, pluricellular, to about 1 mm. long, rarely broadened and somewhat scale-like at the base; leaves to 3 m. long, erect, or the larger ones scandent, petiolate, elongated; petiole castaneous to atropurpureous, amply to sparsely pubescent (to glabrate), the trichomes rigid, spreading, pluricellular, lustrous, castaneous; lamina 4- to 5-pinnate, firm-herbaceous, glabrous to sparsely pubescent, the trichomes castaneous to yellowish brown, spreading; rachis castaneous to (distally) yellowish brown, glabrous to sparsely pubescent, flexuous (commonly sharply and conspicuously so); pinnae numerous, stalked, spreading to ascending, deltoid-lanceolate, at least the larger ones inequilateral at base (more strongly produced basiscopically), the

costa slightly to strongly flexuous; ultimate segments entire or bifid to deeply lobed, elongated, narrow-elliptic to oblanceolate, often retuse at apex, the margin somewhat thickened into a slightly cartilaginous, continuous rim; veins simple (in entire segments) or 1-forked (in lobed segments), their tips not or slightly enlarged, terminating at or short of the segment margin.

Alice Tryon (1970) has described var. *galeanus*, from Guerrero, Mexico, as differing from the typical variety in its more delicate, erect leaves, and its tan or light-brown (rather than deep-brown to black) rhizome scales.

Eriosorus hirtus (HBK) Copel. Gen. Fil. 58. 1947. *Grammitis hirta* HBK, Nov. Gen. et Sp. 1: 4 (Fol. ed.) 1816. *Gymnogramma hirta* (HBK) Kaulf. Enum. Fil. 72. 1824. *Psilogramma hirta* (HBK) Kuhn, Fests. 50 Jubil. Reals. Berlin: Chaetop. 338. 1882. *P. chiapensis* Maxon, Bull. Torrey Bot. Club 42: 81. 1915 (type from Chiapas, Mexico, *Purpus* 6722). *Gymnogramma chiapensis* (Maxon) C. Chr. Index Fil. Suppl. Prelim. 19. 1917.

Apparently represented in Guatemala by a single collection: in damp, shaded ravine, Sierra de los Cuchumatanes, Dept. Huehuetenango; alt. 2,600-2,700 m. (*Steyermark* 51954). Cuba; southern Mexico; Honduras; Venezuela; Bolivia.

Rhizome slender to rather stout, provided with stout, terete, subappressed, bristle-like trichomes, these lustrous, castaneous to blackish, pluricellular, to 2 mm. long; leaves erect, less than 1 m. long, long-petiolate; petiole castaneous to atropurpureous, sparsely to densely provided with spreading, castaneous, articulated trichomes; lamina deltoid-lanceolate, 2-pinnate to nearly 3-pinnate-pinnatisect (never truly 3-pinnate, as stalks of the tertiary segments are always alate and adnate), firm-herbaceous, moderately to densely pubescent on axes and both surfaces, the trichomes spreading, pale yellow or yellowish brown; rachis castaneous to atropurpureous, straight to slightly flexuous; pinnae 10-15 pairs, short-stalked, slightly ascending, narrowly to broadly deltoid, at least the proximal ones inequilateral at base (more strongly produced basiscopically), the costa not or scarcely flexuous; ultimate segments cuneate, often lobed or bifid, frequently retuse at apex, the margin not or weakly differentiated, the rim, if any, thin and inconspicuous; veins terminating at or very near the segment margin.

The Andean variety *glandulosus* A. F. Tryon differs in its deltoid lamina which is nearly as broad as long, and in the trichomes, which bear a globose, apical cell.

Eriosorus hispidulus (Kunze) Vareschi, Fl. Venez. 1: 640. 1969. *Jamesonia hispidula* Kunze, Bot. Zeit. 2: 739. 1844. *Gymnogramma hispidula* (Kunze) Kl. Linnaea 20: 407. 1847. *Psilogramma hispidula* (Kunze) Kuhn, Fests. 50 Jubil. Reals. Berlin: Chaetop. 341. 1882.

Apparently represented in Guatemala by a single collection: crevices of shaded, moist rocks, on Cerro Brujo, Dept. Chiquimula, alt. 1,700-



FIG. 32. *Eriosorus*. a-b, *E. hirtus* var. *hirtus*: a, habit, $\times \frac{1}{2}$; b, a middle pinnule, adaxial surface, $\times 12$; c-d, *E. hispidulus* var. *hispidulus*: c, apical portion of lamina, $\times \frac{1}{2}$; d, pinna apex, abaxial surface, $\times 6$; e, *E. flexuosus* var. *flexuosus*, portion of lamina, $\times \frac{1}{2}$.

2,000 m. (*Steiermark 30990*). Puerto Rico; Colombia to British Guiana.

Rhizome slender to rather stout, provided with stout, terete, subappressed, bristle-like trichomes, these lustrous, castaneous to blackish, pluricellular, to 2 mm. long; leaves erect, to about 50 cm. long, long-petiolate; petiole castaneous to atropurpureous, sparsely to densely provided with spreading, castaneous, articulated trichomes; lamina sometimes slightly dimorphous (mature fertile segments somewhat constricted), linear to deltoid-lanceolate, 2-pinnate to (rarely) nearly 3-pinnate, firm-herbaceous to subcoriaceous, moderately to densely pubescent on axes and both surfaces, the trichomes spreading, clear to yellowish brown; rachis castaneous to atropurpureous, straight to slightly flexuous; pinnae 10-20 pairs, short-stalked, spreading to slightly ascending, narrowly to broadly deltoid, subequilateral; pinnules 3-7 pairs, adnate (or basal ones free), cuneate, suborbicular to ovate or obovate, subentire to crenate or (rarely) deeply pinnatisect, the margins strongly differentiated, with a continuous, conspicuous, yellow, subcartilaginous rim, plane or often somewhat revolute; veins pinnately branched in the pinnules, terminating well short of the margin, the tips somewhat enlarged.

GRAMMITIS Swartz

REFERENCES: W. R. Maxon, Notes upon *Polypodium duale* and its allies, Contr. U.S. Natl. Herb. 17: 398-406. 1914, and *Polypodium trichomanoides* and its American allies, *tom. cit.* 542-557. E. B. Copeland, The American species of *Xiphopteris*, Amer. Fern J. 42: 41-52, 93-110. 1952, and *Grammitis*, Philipp. J. Sci. 80: 93-271. 1952, and *Ctenopteris* in America, *op. cit.* 84: 381-475. 1956. C. V. Morton, The genus *Grammitis* in Ecuador, Contr. U.S. Natl. Herb. 38: 85-123. 1967.

Plants small to medium-sized, commonly epiphytic, occasionally epipetric, rarely terrestrial; rhizome creeping to ascending or erect, commonly scaly (rarely naked), the scales nonclathrate or, occasionally, clathrate; leaves monomorphic, or in a few species the fertile portion modified, erect to pendent, sessile to long-petiolate; petiole not articulate, lacking scales, rarely completely glabrous, but typically provided with spreading, castaneous, unicellular trichomes, these 0.4-2 mm. long; lamina thin-herbaceous to coriaceous, typically pinnatisect (rarely simple and entire, occasionally fully pinnate) and tapering to apex and base, the tissue and/or rachis commonly provided with spreading, unicellular trichomes as on the petiole, but lacking scales; segments (or pinnae) usually numerous, spreading at right angles, or somewhat ascending; veins free, or in a few species anastomosing to form costal areoles, simple and rudimentary to forked, or pinnately branched; sori round to elongated, borne along or at the tips of veins or their branches, typically discrete, but often confluent at maturity, superficial to deeply immersed in the tissue (but never confluent in a deep, central groove); indusium lacking; paraphyses essentially lacking; sporangia stalked, glabrous to setose; spores trilete, tetrahedral, or globose-tetrahedral, commonly pale green (containing chlorophyll), apparently without perine.

Several species of *Grammitis* are beset with conspicuous, black, clavate fungi. These are usually about 1 mm. long and are easily observed growing on the rachis, the costae, or among the sori. The fungal

growth so consistently occurs on these species that it can be used rather effectively as a diagnostic character. I have found it almost invariably on the Guatemalan species of *G. anfractuosa*, *G. semihirsuta*, and *G. subtilis*. Furthermore it is just as common on *G. taxifolia* (L.) Proctor (found in the West Indies and from Costa Rica to Bolivia and Brazil). The fungus is an ascomycete, described as *Acrospermum maxonii* Farlow ex Riddle (Mycologia 12: 175-181. 1920), and is named in honor of Maxon, who first brought it to Farlow's attention. Maxon found the growth occurring on many collections of *Polypodium induens* (= *G. anfractuosa*) and on the Jamaican *P. cretatum* (= *G. subtilis*?). I am indebted to Dr. Alan R. Smith, University of California, Berkeley, for providing me with the reference to the publication.

Although the species of *Grammitis* were long absorbed in the broad concept of *Polypodium*, workers now are generally agreed that the characters separating the genera are fairly clear and constant (see Morton [1967] for a good discussion of the history of the problem). That the former be placed in a separate family, Grammitidaceae, as some authors suggest, appears to me to be ill-advised, and I agree with Morton's observation that "this is an extreme view to take of plants that, in some instances, can hardly be distinguished from one another." In the present treatment species of former genera, *Ctenopteris*, *Xiphopteris*, and *Glyphotaenium* are included with *Grammitis*. Except for the latter, these genera were each distinguished on the basis of such quantitative characters as degree of dissection of lamina or number of vein branches. The few species of *Glyphotaenium* have been considered distinct due to their impressed sori and the merging of basal vein branches to form costal areoles. But sori impressed (in varying degrees) are hardly uncommon in *Grammitis*, and there are at least a few species in other sections in which there is some casual anastomosing of veins.

The concept of *Grammitis*, as herein accepted, can thus be said to differ from that of *Polypodium* in the following principal characters. Petioles are not (or obscurely) articulate to the rhizome; unicellular, spreading, usually dark and conspicuous trichomes (setae) are commonly found on the petiole and lamina, but scales are lacking (except around the petiole base); spores are trilete and pale green (containing chlorophyll). In contrast, species of *Polypodium* have the petiole articulate to the rhizome; scales are commonly found on some part(s) of the leaf, but "grammitid" setae are absent; spores are monolete and brown to tawny (or at least not green). In addition there are some minute, but significant, differences in gametophytes and sporangial stalks which further distinguish the genera.

Thus circumscribed, *Grammitis* is a pantropical genus containing about 400 species, most of which are rather small epiphytes. It is strongly represented in Guatemala.

- a. Leaves entire to repand or very shallowly lobed; fertile portion of lamina unmodified.
 - b. Leaves (10) 12-40 cm. long; veins commonly forming a series of costal areoles; sori very deeply impressed in the tissue. *G. harrisii*.
 - b. Leaves 1.5-9.5 cm. long; veins free; sori superficial, or very slightly impressed in the tissue.
 - c. Rhizome scales numerous; leaves 6-9.5 cm. long, 0.5-0.9 cm. broad, with sori well-spaced between costa and margin. *G. minuscula*.
 - c. Rhizome scales lacking; leaves 1.5-5 (7) cm. long, 0.2-0.4 cm. broad, with sori nearly or quite filling the area between costa and margin. *G. jungermannioides*.
- a. Leaves deeply lobed to pinnate, or in a few species the modified, fertile, distal portion of the lamina subentire.
 - d. Veins of ultimate segments simple, or with a single branch; segments each with a single sorus (in a few species sori confluent and forming a solid mass along the rachis in a modified, subentire, apical portion of the lamina).
 - e. Fertile (proximal) portion of lamina conspicuously modified (caudate or subentire).
 - f. Petiole and lamina provided with castaneous, spreading trichomes; rhizome scales subclathrate, terminating in a castaneous seta; hydathodes commonly conspicuous adaxially. *G. skutchii*.
 - f. Petiole and lamina essentially glabrous; rhizome scales not clathrate, lacking an apical seta; hydathodes vestigial or lacking. *G. serrulata*.
 - e. Fertile portion of lamina unmodified (or in *G. delitescens* often less deeply lobed than the sterile portion, but never subentire).
 - g. Leaves densely provided with conspicuous, long (to 2 mm.), spreading, castaneous trichomes; rhizome scales yellow to deep orange (or sometimes with a castaneous margin).
 - h. Margins of rhizome scales conspicuously long-setose. ... *G. blepharodes*.
 - h. Margins of rhizome scales subentire, or minutely denticulate, never setose.
 - i. Segments obtusely triangular, obliquely ascending, most of them 1-1.5 times as long as broad. *G. basiattenuata*.
 - i. Segments oblong, with sides subparallel, usually spreading at a right angle from the rachis, most of them 2-2.5 times as long as broad.
 - j. Veins unbranched, thus only a single hydathode present on the adaxial surface of the segment; segments not (or scarcely) gibbous; rhizome scales 1-1.5 mm. long. *G. cookii*.
 - j. Veins 1-forked, both tip and branch terminating in a hydathode; segments often gibbous acroscopically at base; rhizome scales 2-4 mm. long. *G. trichomanoides*.
 - g. Leaves glabrate or sparsely provided with short (0.1-0.4 mm.) trichomes, or if long-pilose then the trichomes whitish or tawny; rhizome scales blackish to grayish brown or castaneous.
 - k. Leaves densely long-pilose abaxially (especially along the rachis), the trichomes ca. 1 mm. long, spreading, tawny; sporangia conspicuously setose. *G. mitchellae*.
 - k. Leaves sparsely puberulent or short-pilose (especially along the rachis), the

trichomes 0.1-0.4 mm. long, pale to castaneous, spreading to subappressed; sporangia glabrous.

- l. Rachis sparsely puberulent, the trichomes pale yellow to tawny, flattened and often twisted, 2- to 4-celled; fertile portion of lamina often less deeply lobed than the sterile; most segments broad-triangular. *G. delitescens*.
- l. Rachis sparsely short-pilose (especially abaxially), the trichomes mostly castaneous, terete, unicellular; fertile portion of lamina unmodified; most segments oblong to narrow-triangular. *G. limula*.
- d. Veins of ultimate segments pinnately arranged (*i.e.*, each segment bearing a midrib with 2 or more vein branches); segments each commonly bearing 2 to many, mostly discrete, sori.
- m. Rachis and pinnae glabrous, or sparsely and minutely puberulent with appressed, glandular trichomes, these scarcely visible, never more than 0.1 mm. long (very rarely intermixed with a few, scattered, long, spreading ones).
- n. Lamina lax, membranaceous; pinnae ascending, inequilateral at base, larger ones 3-4 times as long as broad; rhizome scales 0.7-1.5 mm. long. *G. dissimulans*.
- n. Lamina rigid, coriaceous; pinnae spreading at right angles, subequilateral at base, most of them as broad as long; rhizome scales 1.5-4 mm. long. *G. moniliformis*.
- m. Rachis and/or petiole sparsely to densely pilose or hirsute with spreading trichomes, these 0.3-4 mm. long (in a few species intermixed with scattered, minute, pluricellular or glandular ones).
- o. Rhizome scales lacking (in *G. mollissima*), or sparsely to abundantly setose or ciliate (cilia often inconspicuous in *G. kalbreyeri*).
- p. Leaves obviously petiolate; petiole (4) 5-20 cm. long, (0.3) 0.4-1.8 mm. thick; lamina pectinate, larger segments 3-8 times as long as broad; acute or subacute.
- q. Sori inframedial to medial; sporangia setose.
- r. Rhizome scales deep orange to castaneous, their margins provided with long setae, these often as long as the scale; sporangia bearing 1-3 short setae, these rarely as long as the sporangial capsule; petiole short, $\frac{1}{2}$ - $\frac{1}{6}$ as long as the lamina. *G. asplenifolia*.
- r. Rhizome scales yellow to pale orange, their surfaces (as well as margins) densely short-setulose; sporangia with a single, long seta, this commonly as long as the capsule and stalk combined; petiole (at least on fertile leaves) often as long as the lamina. *G. lehmanniana*.
- q. Sori supramedial to submarginal; sporangia glabrous.
- s. Lamina broadest at base, chartaceous to subcoriaceous; petiole commonly equaling the lamina; costa and veins immersed, obscure. *G. kalbreyeri*.
- s. Lamina somewhat or greatly reduced at base, firm-herbaceous; petiole $\frac{1}{3}$ - $\frac{1}{4}$ the length of the lamina; costa and veins commonly distinct. *G. semihirsuta*.
- p. Leaves sessile or very short-petiolate; petiole 0.5-2 (3) cm. long, 0.1-0.4 mm. thick; lamina not pectinate, pinnae 1-2 (3) times as long as broad, obtuse to subacute.
- t. Sporangia conspicuously setose.
- u. Rhizome scales present; plants growing at 1,500-3,300 m.; larger pinnae (5) 7-20 mm. long. *G. cultrata*.

- u. Rhizome scales lacking; plants growing at 50-1,000 m.; larger pinnae 4.5-7 mm. long. *G. mollissima*.
- t. Sporangia glabrous (sometimes setose in *G. heteromorpha* outside of Guatemala).
- v. Leaves (6) 10-70 cm. long, commonly (at least in Guatemala) dichotomously forked; pinnae, especially proximal ones, short-stalked, cuneate at base. *G. heteromorpha*.
- v. Leaves 3-10 (12) cm. long, never forked; pinnae adnate, often slightly decurrent. *G. subtilis*.
- o. Rhizome scales naked, or glandular-puberulent, but never with conspicuous setae or cilia on scale surface or margins.
- x. Rhizome scales yellow to orange, nonclathrate, minutely glandular-puberulent; lamina thin-herbaceous. *G. delicatula*.
- x. Rhizome scales grayish brown to blackish, clathrate or subclathrate, naked; lamina firm-herbaceous to subcoriaceous.
- y. Rhizome scales inconspicuous, 0.5-1.3 mm. long; sori 1-4 per segment; larger pinnae (segments) mostly 1.5-2 times as long as broad. *G. anfractuosa*.
- y. Rhizome scales conspicuous, 2-5 mm. long; sori (4) 6-24 per segment; larger pinnae (segments) mostly 4-8 times as long as broad.
- z. Pinnae mostly wide-spaced; sori 12-24 per pinna. *G. firma*.
- z. Pinnae (segments) mostly crowded; sori 4-10 (12) per pinna.
 - aa. Segments strongly ascending (45-60°), essentially glabrous; dark, spreading trichomes on petiole and rachis 0.2-0.8 mm. long; petiole not marginate. *G. leptostoma*.
 - aa. Segments spreading or slightly ascending (75-90°), with dark, spreading trichomes on petiole and/or rachis mostly 1-2 mm. long; petiole often marginate on both sides for much of its length. *G. pilosissima*.

Grammitis anfractuosa (Kze. ex Kl.) Proctor, *Rhodora* 63: 35. 1961. *Polypodium anfractuosum* Kze. ex Kl. *Linnaea* 20: 375. 1847. *P. induens* Maxon, *Bull. Torrey Bot. Club* 32: 75. 1905. *Ctenopteris anfractuosa* (Kze. ex Kl.) Copel. *Philipp. J. Sci.* 84: 431. 1956.

In forests and wooded ravines, on tree trunks, 900-2,500 m.; Alta Verapaz; Chiquimula; El Progreso; El Quiché; Santa Rosa; Zacapa. Greater Antilles; Guadeloupe; southern Mexico; Honduras; El Salvador to Panama; Colombia to British Guiana; Ecuador; Peru.

Rhizome wiry, slender, stoloniferous, at the apex sparsely provided with inconspicuous, ovate or lanceolate scales, these 0.5-1.3 mm. long, glabrous, gray-brown to blackish, subclathrate; leaves 5-14 cm. long, 0.6-1.5 cm. broad, subsessile or short-petiolate; petiole 0.3-1.5 cm. long, 0.3-0.4 mm. thick, terete, gray-brown to blackish, sparsely to amply provided with spreading, unicellular, castaneous trichomes, these 0.4-1 mm. long; lamina deeply pinnatisect, cut almost entirely to the rachis, firm-herbaceous to chartaceous, linear or narrow-elliptic, tapering strongly at both ends, the apex often short-caudate; rachis blackish, amply provided with spreading trichomes as on the petiole; segments 12-24 pairs, spreading (mostly at right angles), acute to obtuse, larger ones 2-7

mm. long, 1-3 mm. broad, oblong to triangular, the margins entire, plane or (more commonly) somewhat revolute, the abaxial surface commonly bearing some spreading, castaneous, unicellular trichomes, especially among the sori and on the margin; costae indistinct, often flexuous; veins obscure, 1-2 pairs, simple, often rudimentary, terminating well short of the margin in slightly dilated tips; sori 1-4, borne at or near the vein tips, superficial, round, discrete, but sometimes confluent at maturity, inframedial; sporangia glabrous.

Grammitis asplenifolia (L.) Proctor, Brit. Fern Gaz. 9: 76. 1962. *Polypodium asplenifolium* L. Sp. Pl. 1084. 1753. *P. suspensum* var. *asplenifolium* (L.) Krug, Bot. Jahrb. Syst. 24: 127. 1897. *P. suspensum sensu* Jenm. Ferns Brit. West Ind. & Guiana 269. 1908 (not L. 1753). *Ctenopteris asplenifolia* (L.) Copel. Gen. Fil. 219. 1947.

In forests or wooded ravines, pendent from trunks of trees or tree ferns (typically the petiole spreading, and the lamina drooping), 800-2,200 m.; Alta Verapaz; Baja Verapaz; Guatemala; Huehuetenango; Zacapa. West Indies; southern Mexico to Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Rhizome short-creeping to ascending, abundantly scaly, the scales lanceolate, ovate or elongate-triangular, 0.8-2 (3) mm. long, highly lustrous, deep orange to castaneous, not or scarcely clathrate, the margins and apex amply and conspicuously setose, the long, spreading setae orange or castaneous, often as long as or longer than the scale; leaves 25-60 cm. long, 3-7 cm. broad, long-petiolate; pendent, or the petiole spreading horizontally, sharply bent at apex and the lamina drooping; petiole 10-30 cm. long, on fertile leaves nearly as long as (occasionally slightly longer than) the lamina, stout, 0.4-1.2 mm. thick, terete, brown to atropurpureous, sparsely to abundantly provided with long, silky, spreading, unicellular trichomes, these 1-3 mm. long, tawny to orange; lamina thin-herbaceous, lanceolate, pectinate, cut nearly to the rachis, gradually reduced to apex, scarcely reduced at base, rachis and tissue amply provided with orange to castaneous, spreading trichomes; segments numerous, mostly perpendicular to the rachis, narrowly deltoid, acute, dilated subequally at base or more strongly decurrent basiscopically, with margins entire and essentially plane, larger ones 1-4 cm. long, 0.4-1.4 cm. broad at the dilated base, basal (and rarely the next) pair slightly to somewhat reduced, costa distinct to indistinct, often flexuous; veins obscure, terminating well short of the segment margin, simple, but fertile ones with a rudimentary, medial spur on which the sorus is borne, the tips slightly dilated, hydathodes lacking or minute and indistinct; sori discrete, round, inframedial between costa and margin, not impressed in the tissue, 6-20 on each segment; sporangia setose, the setae 1-3, pale, rarely as long as the sporangial capsule.

This is often found in herbaria determined as "*Polypodium suspensum*." However, *Grammitis suspensa* (L.) Proctor is a distinctly different plant, occurring in the West Indies, southern Central America, and northern South America. It is a much more rigid and erect fern, with very short petiole, lamina narrowed at base, sori somewhat impressed, and neither sporangia nor rhizome scales bearing

setae. A more complete explanation of the problem can be seen under C. V. Morton's discussion of *P. flabelliforme* Poir. (Contr. U.S. Natl. Herb. 38: 57-58. 1967).

Grammitis asplenifolia is easily confused with *G. lehmanniana*, under which see further discussion.

Grammitis basiattenuata (Jenm.) Proctor, Bull. Inst. Jamaica Sci. Ser. 5: 32. 1953. *Polypodium basiattenuatum* Jenm. Bull. Bot. Dept. Jamaica II. 4: 114. 1897. *Xiphopteris basiattenuata* (Jenm.) Copel. Amer. Fern J. 42: 104. 1952.

Apparently represented thus far in Guatemala by a single collection: Contreras 5061, in high forest, Nebaj, El Quiché, ca. 2,400 m.; elsewhere on branches and trunks of trees, 1,900-2,500 m. Mexico (Chiapas); Jamaica.

Rhizome erect or ascending, provided with lanceolate or linear-lanceolate, subclathrate scales, these 1.5-2.5 mm. long, yellowish to deep orange, with margins entire, or often remotely and irregularly toothed; leaves 4-12 cm. long, 0.4-0.8 cm. broad, sessile or very short-petiolate; petiole often lacking, or rarely to 1 cm. long; lamina linear or linear-elliptic, tapering at both ends, rather abruptly so at apex, very gradually so at base and long-decurrent, deeply pinnatifid, abundantly provided with spreading, castaneous, unicellular trichomes, these often to 2 mm. long, and frequently intermixed on the abaxial surface with minute (0.1-0.2 mm.), pluricellular, glandular trichomes; segments numerous, most of them broadly and obtusely triangular, 1-1.5 times as long as broad, obliquely ascending, sides (especially the basiscopic) strongly spreading at base, the proximal segments gradually diminishing to very broad, low teeth; veins obscure, 1-forked (or sometimes simple in sterile segments), the branch very short or vestigial, both tip and branch terminating in a usually distinct hydathode; sori round, discrete, one to a segment, borne on the vein branch; sporangia glabrous.

Grammitis blepharodes (Maxon) Seymour, Phytologia 31: 173. 1975. *Polypodium blepharodes* Maxon, Contr. U.S. Natl. Herb. 17: 407. 1914. *Xiphopteris blepharodes* (Maxon) Copel. Amer. Fern J. 42: 109. 1952.

In forests or wooded ravines, on trunks and branches of trees, 300-1,600 m.; Alta Verapaz; Izabal; El Quiché. Southern Mexico; Honduras; Nicaragua; Costa Rica; Panama.

Rhizome relatively stout, erect to ascending, provided with lanceolate to ovate scales, these 1.5-2 mm. long, scarcely or obscurely clathrate, yellow to deep orange (or sometimes dark brown at the margin), and bearing a number of rigid, castaneous, spreading trichomes; leaves 4-18 cm. long, 0.3-0.7 cm. broad, short-petiolate; petiole 0.5-1.5 cm. long, terete, yellowish to grayish brown, this and the lamina abundantly provided with spreading, castaneous, unicellular trichomes, these often to 2 mm. long; lamina linear, firm-herbaceous, cut nearly or quite to the rachis, tapering gradually to a pinnatifid apex, reduced rather abruptly at base; segments spreading at right angles to



FIG. 33. *Grammitis*. a, *G. jungermannioides*, habit, $\times \frac{1}{2}$; b, *G. pilosissima*, habit, $\times \frac{1}{2}$; c-d, *G. blepharodes*: c, habit, $\times \frac{1}{2}$; d, middle portion of lamina, $\times 6$; e, *G. mollissima*, pinnae, $\times 6$.

the rachis, broadly to narrowly oblong, obtuse to subacute; veins obscure, arising from the rachis at an oblique angle, 1-forked (or sometimes simple in sterile segments), the vein tip and its branch each terminating in a distinct, often blackish, hydathode; sori round, discrete, 1 to a segment, borne on the vein branch; sporangia glabrous.

Grammitis cookii (Underw. & Maxon) Seymour, *Phytologia* 31: 173. 1975. *Polypodium cookii* Underw. & Maxon, *Contr. U.S. Natl. Herb.* 17: 408. 1914. *Xiphopteris cookii* (Underw. & Maxon) Copel. *Amer. Fern J.* 42: 98. 1952.

Known in Guatemala only from the type collection: *Cook & Griggs 80*, near Finca Sepacuité, Alta Verapaz, 1902; also represented by a few collections from Costa Rica.

Rhizome rather slender, erect, provided with lanceolate, subelathrate scales, these 1-1.5 mm. long, yellowish to orange, glabrous, subentire; leaves 4-18 cm. long, 0.4-0.8 cm. broad, subsessile to very short-petiolate; petiole 0.5-1.5 cm. long, terete, yellowish or grayish brown, this and the lamina amply provided with spreading, castaneous, unicellular trichomes, these to 2 mm. long; lamina linear-elliptic, tapering rather abruptly to apex and base, deeply pinnatifid, often sparsely and minutely puberulent, the tiny (0.1-0.2 mm.), pluricellular, glandular trichomes intermixed with the long, unicellular ones; segments numerous, spreading at a right angle from the rachis, broadly to narrowly oblong, mostly 2-2.5 times as long as broad, usually with subparallel sides; veins obscure, simple, terminating well short of the segment apex in a distinct hydathode; sori one to a segment, round, discrete, borne at the vein tip; sporangia glabrous.

This and *G. trichomanoides* are doubtfully distinct. The few distinguishing features are merely quantitative—not especially significant. Rhizome scales are nearly identical, except those of *G. cookii* are slightly smaller. Most veins in *G. trichomanoides* branch strongly near the base acroscopically, and at this point many segments are swollen as if to accommodate the long branch and the sorus borne upon it. However a number of smaller, sterile segments are undifferentiated, with simple veins, and these closely resemble segments of *G. cookii*.

One interesting character (shared with *G. basiattenuata*) is so microscopic that it easily escapes detection. The segment surface, especially abaxially, is frequently provided with minute (0.1-0.2 mm.), glandular trichomes, which are usually tortuous and 3- to 4-cellular. These are often deciduous, but with close observation and high magnification can be seen intermixed with the typical, long, spreading, grammitid trichomes, and may in fact be mistaken as remnants of the latter. Maxon, in a discussion of *Polypodium setulosum* Rosenst. (*Contr. U.S. Natl. Herb.* 17: 554. 1916), briefly referred to such "glandular hairs" as occurring also in *G. trichomanoides*. However I have carefully examined all specimens of the latter at my disposal, and have found none.

Grammitis cultrata (Willd.) Proctor, *Rhodora* 63: 35. 1961. *Polypodium cultratum* Willd. Sp. Pl. 5: 187. 1810. *P. senile* Fée, Mém. Fam. Foug. 7: 60, t. 25, f. 1, 1857. *Ctenopteris senilis* (Fée) Copel. Philipp. J. Sci. 84: 398. 1956. *G. senilis* (Fée) Morton, Contr. U.S. Natl. Herb. 38: 103. 1967.

In forests or wooded ravines, commonly pendent from trunks or branches of trees, 1,500-3,300 m.; Alta Verapaz; Baja Verapaz; Chiquimula; Huehuetenango; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Zacapa. Jamaica; Hispaniola; southern Mexico to Panama; Colombia and Venezuela south to Brazil and Bolivia; (Madagascar; Reunion; Mauritius, Seychelles?).

Rhizome slender, erect, densely pilose, and entangled with stout roots, provided (sometimes sparsely so) with castaneous to deep orange, subclathrate scales, these 0.6-1.5 mm. long, ovate to lanceolate, copiously setose, the setae long, rigid, whitish or tawny; leaves usually pendent, subfasciculate, 8-45 cm. long, 1-4 cm. broad, very short-petiolate; petiole 0.8-3 cm. long, 0.2-0.5 mm. thick, terete, brown to blackish, copiously provided with long, silky, spreading, unicellular trichomes, these orange or tawny, 1-1.5 mm. long; lamina thin-herbaceous, linear to narrow-elliptic, pinnate, tapering gradually at both ends; rachis atropurpureous or blackish, amply pilose, the trichomes like those of the petiole; pinnae numerous, larger ones 5-20 mm. long, 3-7 mm. broad, spreading to slightly ascending, adnate, oblong to broadly and obtusely triangular, often rounded and partly adnate at base acroscopically, short-decurrent basiscopically, the margins entire, plane, abundantly pilose as on the rachis, the trichomes 0.6-2 mm. long, tawny or orange, simple, spreading, but those on the margin more often fasciculate in 2's or 3's; costa blackish, or as often obscure; veins indistinct or obscure, simple, 2-8 pairs, terminating well short of the margin, the tips somewhat dilated into distinct hydathodes; sori discrete, round, medial or inframedial, borne at the vein tips, not impressed in the tissue, 2-10 on each pinna; sporangia conspicuously setose, the setae tawny to whitish, as long as or much longer than the sporangium.

Much confusion has attended the circumscription of this species, and a good revision would be in order. The smaller-leaved plants have been separated by a number of authors under *G. senilis*, with attempts to further justify such a split by pointing out differences in number of veins or the proportion of simple *vs.* fascicled trichomes on pinna margins. However none of these features are truly significant, as none are consistent. On the same rhizome may be found leaves with short or rather elongated pinnae, the longer ones quite naturally having more veins and sori. A close examination of all Guatemalan specimens (and many from other regions) which have come to my attention has revealed that none in the complex have pinnae with *only* simple marginal trichomes. There are always some paired ones. It is true that some plants have a greater abundance of trichomes in fascicles of twos and threes, but this does not appear to be well correlated with any other characteristic.

Another species which has been alternately combined with or separated from *G. cultrata* is *Polypodium elasticum* Bory ex Willd., from Madagascar and nearby islands. I have not seen the type, but from various descriptions and from a few specimens so determined this Old World fern may be the same as *G. mollissima* (that is, essentially *G. cultrata* without rhizome scales). To be certain, one should compare all three types and very closely examine the rhizomes of plants from both New and Old World habitats, to ascertain the presence or absence of scales. However, I suspect that *G. mollissima* should be combined under *G. elastica*, this perhaps to be considered a scaleless variety of *G. cultrata*.

Grammitis delicatula (Mart. & Gal.) Proctor, Brit. Fern Gaz. 9: 219. 1965. *Polypodium delicatulum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15 (5): 35. t. 7, f. 1. 1842. *Ctenopteris delicatula* (Mart. & Gal.) J. Sm. Bot. Voy. Herald 227. 1854. *P. heterotrichum* Bak. in Jenm. J. Bot. Brit. & For. 17: 262. 1879.

In forests (usually coniferous), pendent from logs or tree trunks, 2,500-3,500 m.; Chimaltenango; Huehuetenango; San Marcos; Sololá. Southern Mexico; Jamaica.

Rhizome short-creeping to ascending, provided with appressed, inconspicuous scales, these 0.5-1 mm. long, amorphous, pale yellow to orange, nonclathrate, amply but very minutely glandular-puberulent; leaves 6-20 cm. long, 1-2 cm. broad, short-petiolate; petiole 1.2-3.5 cm. long, 0.2-0.3 mm. thick, terete, yellowish to grayish brown, amply provided with spreading, castaneous, unicellular trichomes, these 1 mm. long and commonly intermixed with minute, 1- to 2-celled glandular ones; lamina pinnate, thin-herbaceous, linear to linear-lanceolate or narrowly elliptic, gradually reduced at apex, and somewhat reduced at base, rachis and pinnae amply provided (as on the petiole) with a mixture of castaneous, unicellular trichomes and minute, pale glandular ones; pinnae numerous, ascending, adnate, usually somewhat decurrent basiscopically, acute or subacute, narrow-oblong, with margins subentire and essentially plane, larger ones 7-10 mm. long, 1.2-2.5 mm. broad, costa distinct or indistinct, blackish, somewhat flexuous; veins obscure, 3-6 pairs, extending halfway to the margin, simple, the tips scarcely dilated, lacking hydathodes; sori discrete, round, medial or inframedial, not impressed, 3-6 pairs, borne on the vein tips; sporangia glabrous.

With this possibly could be included *G. jamesonioides* (Fée) Morton, of Hispaniola and northern South America. Maxon compared the two taxa (Proc. Biol. Soc. Wash. 52: 117-118. 1939), and maintained they were distinct species. However, the features by which he distinguished them appear to me to be too highly variable to be efficacious.

Grammitis delitescens (Maxon) Proctor, Bull. Inst. Jamaica Sci. Ser. 5: 32. 1953. *Polypodium delitescens* Maxon, Bull. Torrey Bot. Club 32: 74. 1905. *Xiphopteris delitescens* (Maxon) Copel. Amer. Fern J. 42: 51. 1952.

In forests, on tree trunks, stumps, or rotting logs, 50-1,800 m.; Alta Verapaz; Baja Verapaz; Chiquimula. Southern Mexico; Honduras; Nicaragua; Costa Rica; Jamaica; Cuba.

Rhizome small, erect or ascending, provided with ovate or lanceolate, clathrate or subclathrate scales, these 1-1.5 mm. long, gray-brown to castaneous, glabrous, entire; leaves 5-10 cm. long, 0.2-0.5 cm. broad, sessile or subsessile; petiole 0-0.5 cm. long, dark brown, terete; lamina linear, or very narrow-elliptic or -oblanceolate, tapering gradually to base, moderately to deeply pinnatifid, but often very shallowly so (sometimes only deeply sinuate) near the apex in the fertile portion, rather sparsely puberulent along the rachis (and occasionally on the segments), the trichomes minute (0.1-0.2 mm.), pale yellow to tawny, flattened and often twisted, 2- to 4-celled; segments numerous, most of them broadly triangular, obtuse to acute, near the apex in fertile portion of lamina often becoming mere lobes or (rarely) broad serrations; veins distinct to obscure, simple, terminating in a pale or dark hydathode; sori round to somewhat elongated, at maturity crowded, and often nearly confluent, one to a segment, borne along the vein; sporangia glabrous.

This often has been confused with *G. myosuroides* (Sw.) Sw., of Jamaica, and with good reason. The distinguishing features are either minute or scarcely definitive. In *G. myosuroides*, the lamina is conspicuously differentiated into an entire or subentire apical fertile section, and a pinnatifid distal portion in which the segments are mostly narrow and oblong. In *G. delitescens* the lamina is sometimes unmodified, but most commonly it is moderately differentiated, *i.e.*, the sterile, distal portion is deeply pinnatifid, with segments mostly broad and triangular, while the apical fertile portion is less sharply dissected (sometimes merely deeply sinuate). The trichomes along the rachis afford a better, though not easily discernible, basis for distinction. In both species they are minute (0.1-0.3 mm.); however, in *G. myosuroides* they are dark, rather rigid and spreading, and unicellular, whereas in *G. delitescens* they are pale, often flattened and twisted, and mostly 2- to 4-celled. Another Guatemalan species, *G. limula*, perhaps is even more closely related to *G. myosuroides*, having the same kind of laminar trichomes, but differing in that the fertile portion of the leaf is not at all modified.

Grammitis dissimulans (Maxon) Seymour, *Phytologia* 31: 178. 1975. *Polypodium dissimulans* Maxon, *Contr. U.S. Natl. Herb.* 10: 502. 1908. *Ctenopteris dissimulans* (Maxon) Copel. *Philipp. J. Sci.* 84: 415. 1956.

On trunks of trees, 1,200-1,650 m.; Alta Verapaz (type from Cobán, on tree trunks, *Tuerckheim* 844); Huehuetenango. Apparently not found outside Guatemala.

Rhizome slender, erect, provided with lanceolate, bright-brown scales, these clathrate, 0.7-1.5 mm. long, entire, glabrous; leaves 7-20 cm. long, 0.7-1.2 cm. broad, short-

petiolate to subsessile; petiole 0.2-1 cm. long, dark brown, terete, glabrous; lamina glabrous, membranaceous, linear or linear-elliptic, tapering at both ends, strongly reduced and decurrent at base, cut fully to the rachis; pinnae 20-35 pairs, somewhat ascending, approximate to subdistant, lanceolate to broadly elliptic, often subfalcate, obtuse to subacute, the margins subentire to crenate or shallowly lobed, inequilateral at base, broadly cuneate acropically, decurrent basiscopically, larger central ones 3-4 times as long as broad; veins distinct to indistinct, commonly flexuous, bearing 3-4 pairs of short branches, these extending about halfway to the margin and terminating in pale, inconspicuous hydathodes; sori several to a pinna, round, very slightly impressed in the tissue, each borne at the tip of a vein branch, often somewhat confluent at maturity; sporangia glabrous.

Grammitis firma (J. Sm.) Morton, Contr. U.S. Natl. Herb. 38: 110. 1967. *Polypodium firmum* Kl. Linnaea 20: 378. 1847 (not Kaulf. 1827). *Ctenopteris firma* J. Sm. Hist. Fil. 184. 1875 (*nom. nov.* for *P. firmum* Kl., not Kaulf.). *P. aromaticum* Maxon, Proc. U.S. Natl. Mus. 27: 743. 1904. *C. aromatica* (Maxon) Copel. Philipp. J. Sci. 84: 418. 1956.

In forests or at edges of forests, on tree trunks, 1,300-1,800 m.; Alta Verapaz; Baja Verapaz; El Quiché. Honduras; Costa Rica; Jamaica; Colombia; Venezuela; British Guiana; Peru; Bolivia.

Rhizome rather stout, erect or ascending, amply provided with spreading, lanceolate, attenuate, bright- or grayish brown, iridescent scales, these 3-5 mm. long, glabrous, clathrate; leaves 7-27 cm. long, 2-6 cm. broad, short-petiolate; petiole 2-6 cm. long, 0.5-0.8 mm. thick, subterete, marginate on both sides for most of its length, yellowish or grayish brown to blackish, sparsely provided with rigid, spreading, unicellular, castaneous trichomes, these 0.3-0.4 mm. long, and often intermixed with minute 2- to 3-celled, twisted ones; lamina pinnate, subcoriaceous, lanceolate or elliptic, tapering abruptly to a pinnatifid, sometimes caudate apex, slightly to strongly reduced at base; rachis blackish, amply provided with spreading, castaneous, unicellular trichomes, these 0.3-0.6 mm. long; pinnae 18-32 pairs, spreading to slightly ascending, often curved, adnate, acute or subacute, dilated subequally at base and often widely separated (especially proximal ones), larger ones 9-25 mm. long, 1.5-3 mm. broad, linear, the margins entire, strongly revolute, with a few rigid, castaneous trichomes among the sori and, occasionally, on the margin; costae distinct, blackish, essentially straight, amply provided with short, rigid, castaneous trichomes; veins obscure, 8-12 pairs, simple, terminating short of the margin in inconspicuous hydathodes; sori 6-12 pairs, borne along the veins, superficial, round, discrete, but somewhat confluent at maturity, inframedial; sporangia glabrous.

This is most closely related to, and may not be truly distinct from, *G. pilosissima*, under which see further discussion.

Grammitis harrisii (Jenm.) A. R. Sm. Proc. Cal. Acad. 8: 230. 1975. *Polypodium harrisii* Jenm. Gard. Chron. III. 27: 241. 1900. *Glyphotaenium harrisii* (Jenm.) Proctor. Bull. Inst. Jamaica Sci. Ser. 5: 31. 1953.

Not reported from Guatemala, but to be expected; elsewhere, in deep forests, pendent from trunks or (often upper) branches of trees;

100-950 m. Southern Mexico; British Honduras; Honduras (?); Nicaragua; Jamaica; Hispaniola.

Rhizome short-creeping to suberect, provided with orange to light-brown, subclathrate scales, these rather flaccid, 2-5 mm. long, linear to lanceolate-attenuate, the margins short-ciliate; leaves (10) 12-40 cm. long; 0.6-1.8 cm. broad, petiolate; petiole 4-8 cm. long, 0.5-0.8 mm. thick, terete, yellowish brown, copiously provided with spreading, castaneous, unicellular trichomes, these 1-2.5 mm. long; lamina narrowly elliptic to oblong-lanceolate, acute or subacute, narrowly to broadly acute at base, spongy, opaque, the margins entire to repand, or very shallowly lobed; costa obscure, immersed in the tissue; veins immersed, obscure, but easily observed when held to light, pinnately branched, essentially free, but the basal branches merging to form narrow, costal areoles, and rarely a few outer branches anastomosing; sori discrete, round to elongated, rather deeply immersed in the tissue, borne in 2-3 irregular lines on each side of the costa; sporangia glabrous.

This and 5-6 other neotropical species have been maintained by some authors in a separate genus, *Glyphotaenium*, based on their impressed sori, entire to shallowly lobed margins, and costal areoles. However, there are a number of species in *Grammitis* with subentire laminae, and nearly as many with sori slightly to deeply impressed. There are even a few (outside Guatemala) with costal areoles. That a half dozen species happen to share all three features in common scarcely justifies their being assigned generic status, separate from *Grammitis*.

Grammitis harrisii appears to be intermediate between, and not strongly distinct from, *G. percrassa* (Bak.) Seymour (West Indies, southern Central America, and South America) and *G. trifurcata* (L.) Copel. (southern Central America). The former has relatively shorter and broader leaves, and rhizome scales which are provided with whitish or tawny, bacilliform glands on the margins and surface. On the other hand, *G. trifurcata* has longer and broader leaves, these usually more deeply lobed, with the petiole darker (castaneous to atropurpureous). However, in Guatemala, *G. harrisii* can scarcely be confused with any other species.

Grammitis heteromorpha (Hook. & Grev.) Morton, Contr. U.S. Natl. Herb. 38: 102. 1967. *Polypodium heteromorphum* Hook. & Grev. Icon. Fil. 1, t. 108. 1829. *Ctenopteris heteromorpha* (Hook. & Grev.) Copel. Philipp. J. Sci. 84: 412. 1956.

In forests or wooded ravines, pendent from tree trunks, or on cave walls or ravine banks, 3,400-4,200 m.; Sacatépéquez; San Marcos. Mexico; Colombia; Ecuador; Peru; Bolivia.

Rhizome (often lacking on herbarium specimens) short-creeping to ascending or erect, provided with castaneous to blackish, nonclathrate scales, these 0.6-2 mm. long, ovate to lanceolate, setose, the setae rigid, tawny or whitish; leaves pendent, densely crowded, often subfasciculate, (6) 10-70 cm. long, 0.4-0.8 cm. broad, very short-petiolate; petiole

1-3 cm. long, 0.2-0.4 mm. thick, terete, yellow- to gray-brown, amply provided with silky, spreading trichomes, these tawny to orange or castaneous, 1-2 mm. long, and sometimes intermixed with scattered, minute (0.1-0.2 mm.), pluricellular, branched, glandular trichomes; lamina thin- to firm-herbaceous, linear, pinnate, gradually to abruptly reduced at apex, very gradually and strongly reduced at base, often 1-3 times dichotomously branched distally; rachis brown to blackish, amply pilose as on the petiole, but the simple trichomes often borne in fascicles of 2-5; pinnae numerous, larger ones 3-5 mm. long and often nearly as broad, somewhat ascending, mostly short-stalked, broadly spatulate to obovate, the margins plane, entire to (infrequently) shallow-lobed, narrowly cuneate at base, abundantly pilose as on the axes, the trichomes borne singly on either surface, but commonly fasciculate in 2's to 5's on the margin; costa commonly obscure; veins obscure, simple, 1-3 pairs, the tips slightly dilated into hydathodes and terminating well short of the pinna margin, the hydathodes occasionally bearing white, circular, calcareous, scales adaxially; sori discrete, round, medial, borne at the vein tips, not or scarcely impressed, (1) 2-5 on each pinna; sporangia glabrous (although often sparsely setose in South American plants).

This is a highly variable species, the extreme geographic variants of which might be misconstrued as distinct species if not compared with representative specimens from all other areas. For example, leaves of Mexican plants are thin-textured, unbranched, and rarely bear white, calcareous deposits on the hydathodes. In Guatemala leaves are thin-textured, commonly forked, and sometimes bear calcareous dots on the hydathodes. South American plants are most variable of all, but typically they have much thicker leaves, forked laminae, and more frequent calcareous dots; pinnae often reach 1.5 cm. in length and may be lanceolate to ovate instead of obovate. There is another variant (Colombia to Peru) which Morton recognized as distinct: *G. variabilis* (Mett. ex Kuhn) Morton. Leaves of the latter are 2-pinnate instead of merely forked, but differ in no other way. I do not feel this is sufficient reason for specific distinction, but perhaps it should be considered a variety of *G. heteromorpha*.

***Grammitis jungermannioides* (Kl.) Ching, Bull. Fan. Mem. Inst. Biol. Bot. 10: 240. 1941 (not Copel. 1947). *Polypodium jungermannioides* Kl. Linnaea 20: 373. 1847.**

Apparently known in Guatemala from a single collection: epiphyte, Cobán, Alta Verapaz (*Hatch & Wilson 226*, 1936); otherwise occurring at 1,600-2,500 m. in Honduras; El Salvador; Costa Rica; Panama; Colombia; Venezuela; Jamaica.

Rhizome short, erect, lacking scales; leaves densely caespitose, 1.5-5 (7) cm. long, 0.2-0.4 cm. broad, subsessile to short-petiolate; petiole 0.2-1.5 cm. long, delicate, terete, sublustrous, grayish brown to blackish, this and the lamina amply provided with spreading, castaneous, unicellular trichomes; lamina oblanceolate, often narrowly so, obtuse to subacute, firm-herbaceous, opaque, the margins subentire or strongly repand; costa distinct or indistinct, not prominulous; veins commonly 1-forked, immersed,

obscure, but usually evident when held to light; sori discrete, oval or circular, superficial, borne in 2 parallel lines, each mature one nearly or quite filling the space between costa and margin.

Grammitis kalbreyeri (Bak.) Morton, Amer. Fern J. 60: 66. 1970.
Polypodium kalbreyeri Bak. Trans. Linn. Soc. London II. 2: 291. 1886.

Apparently represented in Guatemala only by Cook & Griggs 441, near Finca Sepacuite, Alta Verapaz (US), and probably Standley 80692, Volcán Pacaya, Depto. Guatemala, 1,800-2,300 m. (F); elsewhere, in and at edges of forests, on trunks and branches of trees, 1,300-2,100 m. Costa Rica; Colombia; Venezuela; British Guiana; Brazil.

Rhizome short-creeping to ascending, provided at the apex with lustrous, orange scales, these 1-2.5 mm. long, linear, subclathrate, the margins sparsely to amply short-ciliate, the cilia concolorous with the scale body; leaves 10-45 cm. long, 2-10 cm. broad, long-petiolate; petiole 5-24 cm. long, about as long as the lamina, terete, wiry or stout, 0.3-1.8 mm. thick, castaneous to atropurpureous, glabrous distally, toward the base sparsely to copiously provided with spreading, orange to castaneous, unicellular trichomes, these 1-3 mm. long; lamina chartaceous to subcoriaceous, broadly or narrowly triangular, pectinate, cut nearly to the rachis, broadest at base, tapering gradually to a pinnatifid or subcaudate apex, essentially glabrous, or with a few marginal setae, but often the tissue abaxially provided with widely scattered, very minute, appressed trichomes, these 3- to 4-celled, castaneous; rachis essentially glabrous; segments 7-20 pairs, mostly perpendicular to the rachis, oblong-lanceolate to narrowly deltoid, acute or subacute, subequal and slightly dilated at base, the margins entire, essentially plane, larger ones 1.5-5 cm. long, 0.4-0.6 cm. broad, costa immersed, obscure; veins immersed, obscure (even indistinct when held to light), terminating short of the margin, 1-forked on the acroscopic side, the branches long, tips scarcely dilated, hydathodes lacking or rudimentary; sori discrete, round, supramedial to submarginal, borne at the tips of vein branches, very slightly impressed in the segment tissue, 8-20 pairs on each of the larger segments; sporangia glabrous.

With this might be included *G. transiens* (Lindm.) Seymour, of Brazil. The latter apparently lacks the scattered cilia on the rhizome scales, and a number of veins have their branches merging to form oblique areoles, but otherwise the two species can scarcely be separated.

One Guatemalan specimen (Standley 80692) (F) is *G. kalbreyeri* in all respects except for rhizome scales and pinna indument. On this specimen the dark, spreading "grammitid hairs" are rather abundant on the margins and abaxial surfaces of pinnae, whereas in typical *G. kalbreyeri* only a few such trichomes can be found along the margins. Furthermore, on the Standley specimen, the short cilia of the rhizome scales are apparently reduced to unicellular glandlike processes along

the scale margin. Except for these features the specimen exhibits the typical characteristics of *G. kalbreyeri*, e.g., sori supramedial on forked veins, rhizome scales glossy orange, lamina scarcely reduced at base and about equaling the length of the petiole. There is an annotation on this sheet by John Mickel, dated 1973, suggesting this might be a new species. Indeed this might be considered a good variety, based on the characters of rhizome scales and pinna trichomes, if more such specimens were found. However, I hesitate to describe a new variety or species based on a single example, and this collected nearly 40 years ago.

Grammitis lehmanniana (Hieron.) Morton, Contr. U.S. Natl. Herb. 38: 104. 1967. *Polypodium lehmannianum* Hieron. Bot. Jahrb. Syst. 34: 513. 1904 (not *P. lehmannii* Mett. 1857). *Ctenopteris lehmanniana* (Hieron.) Copel. Philipp. J. Sci. 84: 448. 1956.

In forests or wooded ravines, pendent from tree trunks, 600-1,200 m.; Alta Verapaz; Izabal. El Salvador; Costa Rica; Colombia; Ecuador.

Rhizome short-creeping to ascending, abundantly scaly, the scales lanceolate, ovate, or elongate-triangular, 0.5-3 mm. long, somewhat lustrous, yellow to pale orange, clathrate, the surfaces and margins copiously setulose, the setae short, tawny or pale orange; leaves arching or pendent, 35-85 cm. long, 4-8 cm. broad, petiolate; petiole 7-20 cm. long, on fertile leaves $\frac{1}{2}$ - $\frac{1}{4}$ as long as the lamina, 0.6-1.2 mm. thick, terete, yellowish to reddish brown, abundantly provided with long, spreading, unicellular trichomes, these 2-3 mm. long, castaneous; lamina thin- to firm-herbaceous, lanceolate, subpectinate, cut nearly to the rachis, gradually reduced to apex, scarcely reduced at base, rachis and tissue amply provided with orange to castaneous, spreading trichomes; segments numerous, mostly perpendicular to the rachis and joined by a broad, often U-shaped sinus, narrowly deltoid, acute, dilated subequally at base, with margins entire and essentially plane, larger ones 2-4 cm. long, 0.6-1.2 cm. broad at the dilated base, basal (and rarely the next) pair slightly reduced, costa distinct and blackish, often somewhat flexuous; veins obscure, terminating short of the segment margin, simple, but fertile ones with a rudimentary spur on which the sorus is borne, the tips slightly dilated, hydathodes lacking or minute and indistinct; sori discrete, round, inframedial, not impressed, 12-25 on each segment; sporangia bearing a single, long, tawny seta on the annulus, the seta commonly as long as the capsule and stalk combined.

This is easily confused with *G. asplenifolia*, as most of the diagnostic features are rather subtle. For example, both species have setose rhizome scales, but the long setae on *G. asplenifolia* are confined to the scale margin and apex. In *G. lehmanniana* setae are shorter, but more copious, and are borne on the scale surface as well as margins. The scales are rather strongly appressed and are usually so densely packed and setulose that they are at first easily overlooked.

Grammitis leptostoma (Fée) Seymour, Phytologia 31: 179. 1975. *Polypodium leptostomum* Fée, Mém. Fam. Foug. 7: 58, t. 21, f. 2.

1857. *P. productum* Maxon, Contr. U.S. Natl. Herb. 13: 11. 1909 (type from Alta Verapaz, *Tuerckheim II-1347*) (not Christ, 1907).

In forests, on tree trunks, 1,250-1,450 m.; Alta Verapaz. Mexico; El Salvador.

Rhizome short-creeping, provided with spreading, lanceolate, grayish brown, iridescent scales, these 2-3 mm. long, glabrous, subclathrate; leaves 10-24 cm. long, 1-1.5 cm. broad, short-petiolate; petiole 0.5-3 cm. long, 0.3-0.5 mm. thick, terete, yellowish brown to blackish, sparsely to amply provided with spreading, unicellular orange trichomes, these 0.3-0.8 mm. long, and intermixed with minute, 2- to 6-celled, whitish to tawny ones, these 0.05-0.3 mm. long, often forked and gland-tipped; lamina pinnate (at least proximally), firm-herbaceous to chartaceous, linear to linear-lanceolate, tapering at both ends; rachis with mixed indument as on the petiole, but the unicellular trichomes often darker and longer, the pluricellular ones fewer; pinnae (or segments) numerous, essentially glabrous, strongly ascending, adnate, acute, or subacute, larger ones 5-10 mm. long, 1.2-2 mm. broad, narrow-oblong to -triangular, the margins entire, plane or (more commonly) somewhat revolute and often with a few, scattered, minute, 2- to 3-celled glandular trichomes; costae usually distinct, blackish, straight or slightly flexuous; veins obscure, 3-7 pairs, simple, terminating short of the margin in somewhat dilated tips; sori 2-6 pairs, borne at or near the vein tips, not or slightly immersed, round, discrete, but sometimes somewhat confluent at maturity, medial; sporangia glabrous.

Grammitis limula (Christ) L. D. Gómez, Brenesia 8: 47. 1976.
Polypodium limula Christ, Bull. Soc. Bot. Genève II. 1: 218. 1909.

In forests, on tree trunks, 700-1,450 m.; Alta Verapaz. Honduras; Nicaragua; Costa Rica; Panama.

Rhizome small, erect, provided with ovate, gray-brown to blackish scales, these not or scarcely clathrate, 0.4-0.8 mm. long, glabrous, entire, often convexo-concave; leaves 4-14 cm. long, 0.2-0.4 cm. broad, sessile to short-petiolate; petiole 0-1 cm. long, terete, yellowish to grayish brown or castaneous, this and the rachis sparsely to moderately provided with castaneous (rarely paler), spreading, unicellular trichomes, these 0.2-0.4 mm. long; lamina linear or very narrow-elliptic, tapering gradually to base; deeply pinnatifid (often quite to the rachis), the sterile and fertile portions not differentiated as to shape or dissection, essentially glabrous, but occasionally with a few scattered trichomes (as on the rachis) on the abaxial surface; segments numerous, mostly oblong, spreading, toward the base of the lamina gradually reduced and there becoming broadly triangular; veins indistinct or obscure, simple, terminating in a pale or dark hydathode; sori round to elongated, at maturity crowded to subconfluent, one to a segment, borne along the vein; sporangia glabrous.

This may be readily confused with *G. delitescens*, under which see further discussion.

Grammitis minuscula (Maxon) Copel. Philipp. J. Sci. 80: 128. 1951.
Polypodium minusculum Maxon, Contr. U.S. Natl. Herb. 13: 11. 1909.

Known only from the type collection: on a tree trunk in mountains near Cobán, Alta Verapaz, 1,600 m. (*Tuerckheim II-1987*, 1907).

Rhizome erect, sometimes elongated, provided with appressed, yellowish brown, sub-clathrate, lanceolate scales, these about 2 mm. long, entire; leaves 6-9.5 cm. long, 0.5-0.9 cm. broad, obviously petiolate; petiole 1-2.5 cm. long, delicate, terete, dull brown, this and the lamina densely provided with spreading, castaneous, unicellular trichomes; lamina oblanceolate, obtuse to subacute, spongy, opaque, the margins entire to slightly repand; costa obscure, immersed in the tissue; veins 4- to 5-forked, immersed, obscure, but plainly visible when held to light; sori discrete, oval or circular, superficial or very slightly immersed, borne in 2 parallel lines, each one medial to inframedial between costa and margin.

Grammitis mitchellae (Baker) Seymour, *Phytologia* 31: 174. 1975.
Polypodium mitchellae Baker in Hemsl. *Biol. Centr. Amer. Bot.* 3: 664. 1885 (type from Orange Walk, British Honduras, Mitchell *s.n.*).
Xiphopteris mitchellae (Bak.) Copel. *Amer. Fern J.* 42: 97. 1952.

In dense forests, on trunks or branches of trees, or on mossy, rotting logs, 200-900 m.; Alta Verapaz; Izabal. British Honduras; Nicaragua; Costa Rica; Panama.

Rhizome small, erect, provided with ovate or lanceolate, clathrate scales, these 1-1.5 mm. long, gray-brown to blackish, densely long-ciliate; leaves 3-7 cm. long, 0.3-0.6 cm. broad, sessile or subsessile; lamina very narrowly oblanceolate, commonly broadest above the middle, tapering gradually to a decurrent base, moderately to deeply pinatifid, densely pilose, especially along the rachis abaxially, the trichomes ca. 1 mm. long, tawny, spreading, unicellular; segments 12-25 pairs, broadly triangular, obliquely ascending, frequently as broad as long, obtuse, but often appearing acute due to the revolute margins on older leaves; veins obscure, 1-forked (or often simple in sterile segments), the short branch borne near the base, both tip and branch terminating in a pale to dark hydathode; sori round, discrete, or at maturity often becoming confluent, one to a segment, borne on the vein branch; sporangia densely tawny-setose.

Grammitis mollissima (Fée) Proctor, *Rhodora* 63: 35. 1961. *Polypodium mollissimum* Fée, *Mém. Fam. Foug.* 11: 47, *t.* 12, *f.* 2. 1866.
P. suspensum var. *mollissimum* (Fée) Krug, *Bot. Jahrb. Syst.* 24: 127. 1897. *Ctenopteris mollissima* (Fée) Copel. *Philipp. J. Sci.* 84: 423. 1956.

In forests or wooded ravines, 50-1,000 m.; Alta Verapaz; Baja Verapaz; Huehuetenango. West Indies; southern Mexico; Honduras to Panama; the Guianas; Mauritius; Seychelles.

Rhizome slender, erect, densely pilose and entangled with stout roots, but lacking scales; leaves usually pendent, subfasciculate, 5-30 cm. long, 0.7-1.5 cm. broad, very short-petiolate; petiole 0.4-1 cm. long, wiry, 0.2-0.4 mm. thick, terete, castaneous to blackish, copiously provided with long, silky, spreading, unicellular trichomes, these orange or tawny, 1-1.5 mm. long; lamina thin-herbaceous, linear to narrow-elliptic, pinnate, tapering gradually at both ends; rachis blackish, amply pilose, the trichomes like those of the petiole; pinnae numerous, larger ones 4.5-7 mm. long, 2.5-4 mm. broad, spreading to slightly ascending, adnate, oblong to broadly and obtusely triangular, often sharply rounded at base acroscopically, decurrent basiscopically, the margins entire,

plane, abundantly pilose as on the rachis, the trichomes about 1 mm. long, tawny or orange, simple, but those on the margin more often fasciculate in 2's or 3's; costa and veins obscure, the veins simple, 2-3-(4) pairs, terminating well short of the margin, the tips somewhat dilated into distinct hydathodes; sori discrete, round, inframedial, borne at the vein tips, not impressed in the tissue, 3-6 on each pinna; sporangia conspicuously setose, the setae tawny to whitish, as long as or much longer than the sporangium.

This may be synonymous with the Old World *Polypodium elasticum* Bory ex Willd., and this merely a variant of *G. cultrata*, under which see further discussion.

Grammitis moniliformis (Lag. ex Sw.) Proctor, Brit. Fern Gaz. 9: 219. 1965. *Polypodium moniliforme* Lag. ex Sw. Syn. Fil. 33. 1806. *P. melanostictum* Kunze, Linnaea 9: 44. 1834. *Ctenopteris moniliformis* (Lag. ex Sw.) J. Sm. Hist. Fil. 184. 1875. *P. calvum* Maxon, J. Wash. Acad. Sci. 12: 440. 1922. *C. calva* (Maxon) Copel. Philipp. J. Sci. 84: 386. 1956. *G. melanosticta* (Kze.) Seymour, Phytologia 31: 179. 1975.

In forests or in exposed locations on trunks or branches of trees, on fallen logs, or occasionally on rocks or in crevices of rocky cliffs, 700-4,400 m.; Alta Verapaz; Chimaltenango; Guatemala; Huehuetenango; El Progreso; Quezaltenango; San Marcos; Santa Rosa; Sololá; Totonicapán. Greater Antilles; southern Mexico to Panama; Colombia and Venezuela, south to Bolivia and Brazil.

Rhizome rather stout, short- to long-creeping, amply provided with lanceolate, clathrate scales, these 1.5-4 mm. long, bright or grayish brown, glabrous, entire; leaves crowded to widely spaced, 4-22 cm. long, 0.4-1.2 cm. broad, short- to long-petiolate; petiole 0.7-6 cm. long, yellowish to grayish brown, stout, terete, commonly marginate to narrow-alate at least toward the lamina, sparsely to amply provided with minute, often branched, glandular trichomes, these 2- to 3-celled, never more than 0.1 mm. long; lamina linear to very narrowly elliptic, rigid, coriaceous, tapering subequally at both ends, cut nearly or quite to the rachis, commonly glabrous, but rarely with a few long, scattered, rigid, spreading trichomes on the rachis or pinnae abaxially; rachis sparsely and minutely glandular-puberulent as on the petiole; pinnae numerous, rigid, short, nearly perpendicular to the rachis, commonly as broad as long, obtuse to (very rarely) subacute, broadly oblong to semicircular, with entire margins, subequilateral, adnate, spreading from the rachis at nearly the same angle acroscopically as basiscopically; veins immersed, obscure (scarcely or not at all discernible even when held to strong light), bearing 1-2 pairs of short branches which terminate short of the margin in small, dark, often indistinct hydathodes; sori several to a pinna, round, slightly impressed, each borne at the tip of a vein branch, often somewhat confluent at maturity; sporangia glabrous.

Authors have attempted to segregate this into several species or varieties, based on characters such as relative length of pinnae, size and color of scales, relative length of rhizome and crowding of leaves, and shades of color of the tissue. Observation of many dozens of specimens throughout the entire range of distribution has convinced me

that none of the features is consistent. These apparently vary slightly according to elevation of habitat and maturity of the individual plant.

Grammitis moniliformis may be recognized by its rigid, coriaceous, narrow leaves, its often semicircular pinnae, and the apparent lack of "grammitid hairs." (However, rarely, a few long, spreading, castaneous trichomes may be observed on the axes of young plants or among the sori in older ones.) Instead, the indument consists of a sparse to moderate covering of microscopic, glandular trichomes found especially along the axes abaxially. They are 2- to 4-celled, pale, twisted, and often forked. These minute processes are not common in *Grammitis* and are easily overlooked, as they seldom attain a length of 0.1 mm.

Grammitis pilosissima (Mart. & Gal.) Morton, Contr. U.S. Natl. Herb. 38: 114. 1967. *Polypodium pilosissima* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 39. 1842. *Ctenopteris pilosissima* (Mart. & Gal.) Copel. Philipp. J. Sci. 84: 390. 1956. *C. megaloura* Copel. *tom. cit.* 391 (type from Cobán, Alta Verapaz, Guatemala, *Tuerckheim II-1855*).

In forests, on trunks or lower branches of trees, very rarely on mossy cliffs, 300-3,800 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Guatemala; Huehuetenango; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Totonicapán. Mexico; Honduras; Costa Rica; Panama; Colombia; Venezuela; Ecuador; Brazil.

Rhizome long- or short-creeping, or ascending, amply provided at the apex with spreading, lanceolate, grayish brown, iridescent scales, these 2-4 mm. long, glabrous, clathrate to subclathrate; leaves 8-27 cm. long, 1-2.5 (3) cm. broad, short-petiolate; petiole 1.5-6 cm. long, 0.4-0.8 mm. thick, terete, often slightly or strongly marginate for part or most of its length, yellowish brown to blackish, sparsely to amply provided with spreading, unicellular, castaneous trichomes (or glabrate in age), these 1-2 mm. long, and often intermixed with minute, 2- to 4-celled, orange or tawny ones, these 0.05-0.2 mm. long, often forked and gland-tipped; lamina deeply pinnatisect (often nearly pinnate), chartaceous to subcoriaceous, linear or narrow-elliptic, gradually tapering to a pinnatifid, often caudate, apex, abruptly and strongly reduced at base, rachis, costae, and tissue (especially among the sori) sparsely to amply pilose as on the petiole; segments numerous, spreading to somewhat ascending, linear to narrowly triangular, acute or subacute, crowded, joined by narrow, acute sinuses, larger ones 6-14 mm. long, 1.5-2.5 mm. broad, the margins entire or (rarely) somewhat sinuate, plane or (more commonly) strongly revolute; costae distinct (blackish) to indistinct, straight to somewhat flexuous; veins obscure, 3-6 pairs, simple, terminating well short of the margin in small, distinct to indistinct hydathodes; sori 3-6 pairs, borne at or near the vein tips, not or slightly immersed, round, discrete, or somewhat confluent at maturity, medial or inframedial; sporangia glabrous.

This highly variable species is part of a confusing pantropical complex which is much in need of comprehensive study. Closely related

lated taxa have been distinguished principally by relative length of segments and by sparseness or abundance of indument. For example, *G. firma* differs merely in its longer, narrower segments, most of which are rather widely spaced. Conversely, *G. flabelliformis* (syn. *Polypodium rigescens* Bory ex Willd.) of Africa and South America has been distinguished by its nearly glabrous leaves, with shorter and broader segments and fewer sori. Indeed, it is then but a short step to the subglabrous *G. moniliformis*, with its segments often as broad as long and even fewer sori. *Grammitis rigens* (Maxon) Proctor, of the Greater Antilles, is even more similar and perhaps is synonymous with, or at least is a variety of, *G. pilosissima*.

An interesting feature which is common to most of the above species (and to *G. leptostoma* as well) is the second type of indument commonly found on the petiole, rachis, and even pinna margins. Inter-mixed with the dark, spreading, unicellular, "grammitid hairs" also may be found some microscopic, pluricellular ones. These rarely exceed 0.1 mm. in length and are usually pale (tawny or whitish), twisted, or 1-forked, with 2-4 cells, and often glandular. They are easily overlooked and thus have rarely been described in the literature.

***Grammitis semihirsuta* (Kl.) Morton**, Contr. U.S. Natl. Herb. 38: 113. 1967. *Polypodium semihirsutum* Kl. Linnaea 20: 379. 1847. *Ctenopteris semihirsuta* (Kl.) Copel. Philipp. J. Sci. 84: 450. 1956.

In forests or wooded ravines, commonly on tree trunks, 1,900-2,700 m.; Huehuetenango; El Quiché; San Marcos. Southern Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama; Colombia and Venezuela; south to Bolivia and Brazil; Jamaica; Hispaniola.

Rhizome erect, provided with lustrous, castaneous scales, these (2) 3-6 mm. long, not or scarcely clathrate (the lumina long and narrow), the margins sparsely to amply setose, the spreading setae concolorous with the scale body; leaves 15-50 cm. long, 1.5-8 cm. broad, petiolate; petiole 3-14 cm. long, much shorter than the lamina, wiry to stout, 0.6-1.6 mm. thick, terete, yellow-brown to castaneous, amply to abundantly provided with long, silky, spreading, orange, unicellular trichomes, these 1-4 mm. long; lamina firm-herbaceous, lanceolate, oblanceolate, or narrow-elliptic, pectinate, cut nearly or quite to the rachis, reduced to both apex and base, rachis (and sometimes the segment margins) provided with castaneous, spreading trichomes as on the petiole; segments numerous, mostly perpendicular to the rachis, oblong-lanceolate to narrow-deltoid, acute or subacute, subequal and not or slightly dilated at base, the margins entire, plane to somewhat revolute, larger ones 1.2-3.5 cm. long, 0.3-0.5 cm. broad, costa distinct, blackish, straight to subflexuous, veins distinct, simple, terminating short of the margin, the tips dilated into rather conspicuous hydathodes, these adaxially bearing circular, white, calcareous scales; sori discrete, round, supramedial to submarginal, borne at the vein tips, not impressed in the tissue, 8-25 on each segment; sporangia glabrous.

Hieronymus (Bot. Jahrb. Syst. 34: 315. 1904) described var. *fuscosetosa*, from Colombia, Peru, and Guatemala, as differing from the typical in the lamina having rather dense, fuscous pubescence between the veins abaxially. Tissue is glabrous in typical *G. semihirsuta*. The syntype cited from Guatemala (San Miguel Uspantán, El Quiché, Heyde & Lux, ed. Donn.-Sm. 3256) has no such pubescence, nor do any other Central American specimens examined. A number of collections seen from Colombia and Peru are rather densely short-pubescent, and it may be proper to recognize them as a good variety. But if so, the variant is apparently confined to South America.

Grammitis serrulata (Sw.) Sw. J. Bot. (Schrader) 1800 (2): 18. 1801. *Acrostichum serrulatum* Sw. Nov. Gen. Sp. Pl. Prodr. 128. 1788. *Asplenium serrulatum* (Sw.) Sw. Fl. Ind. Occ. 3: 1607. 1806. *Xiphopteris serrulata* (Sw.) Klf. Enum. Fil. 85. 1824. *Polypodium serrulatum* Mett. Fil. Hort. Lips. 30. 1856 (not Sw. 1801). *P. duale* Maxon, Contr. U.S. Natl. Herb. 16: 61. 1912. *Cochlidium serrulatum* (Sw.) Bishop, Amer. Fern J. 68: 80. 1978.

In forests and wooded ravines, sea level to 1,800 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Huehuetenango; Izabal; San Marcos. West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia; tropical Africa.

Rhizome slender, elongated, ascending, provided with lanceolate, brown scales, these 3-4 mm. long, entire, glabrous, nonclathrate; leaves 2-8 cm. long, 0.05-0.25 cm. broad, sessile to very short-petiolate; petiole 0.4 mm. long, terete, on juvenile plants sparsely provided with minute, pale, spreading trichomes, but these very soon deciduous; lamina linear, glabrous, firm-herbaceous, tapering gradually to base, subdimorphous, sterile ones (or proximal sterile portion) serrulate to deeply and sharply serrate, fertile portion (apex or distal half) entire or subentire, this plane or, at maturity, conduplicate; veins simple, strongly decurrent, indistinct to obscure, hydathodes vestigial or lacking; sori solitary at the base of the vein, soon becoming confluent and forming a solid mass the width of the lamina.

This has been included by Bishop in *Cochlidium* (under which see further discussion). Superficially, the solid mass of sori on mature plants resembles the coenosori of *Cochlidium*, but each sorus is actually solitary at the base of a vein, where, as the sporangia mature, it grows and spreads to merge with adjacent ones. Furthermore, the serrate laminae, lack of hydathodes, and creeping rhizome are far more suggestive of *Grammitis* than *Cochlidium*.

Grammitis serrulata and *G. skutchii*, with the fertile portions of the lamina conspicuously modified, should not be confused with any of the Guatemalan species. In both, the fertile, apical section is subentire,

often caudate, in marked contrast to the sterile, proximal portion, which may be serrate to pinnatisect.

Grammitis skutchii (Maxon) Seymour, *Phytologia* 31: 175. 1975.
Polypodium skutchii Maxon, *Proc. Biol. Soc. Wash.* 51: 34. 1938.
Xiphopteris skutchii (Maxon) Copel. *Amer. Fern J.* 42: 51. 1952.

On tree trunks, cupressus forest, 2,500-3,000 m.; Chimaltenango (type from Buena Vista, above Tecpam, *Skutch 96*, 1930). Thus far known only from the type and several other collections at or near the type locality.

Rhizome slender, erect or ascending, provided with lanceolate, subclathrate, scales, these 2-3 mm. long, light or dark brown, glabrous, but with a castaneous, lustrous seta at the apex; leaves 4-11 cm. long, 0.2-0.35 cm. broad, sessile to short-petiolate; petiole 0-2 cm. long, terete, grayish brown, this and the lamina sparsely to amply provided with spreading, castaneous, unicellular trichomes, these commonly with a pale, dilated base; lamina linear, firm-herbaceous, subacute, plane, tapering gradually to base, subdimorphous, sterile ones (or proximal sterile portion) serrate to pinnatifid, fertile portion (apex or distal half) entire or subentire; veins simple, distinct to indistinct or obscure, terminating in rather conspicuous hydathodes; sori at first linear to elliptic; borne along the vein, soon becoming confluent and forming a solid mass, nearly or quite spanning the width of the lamina.

This might be confused with *G. serrulata*, the other species in Guatemala which has the fertile portion of the lamina conspicuously modified. The characters used in the key to separate the two, though minute, are consistent. One additional character may be noted, however, which is more obvious, but not always consistent. Fertile laminae in *G. skutchii* are always plane, whereas in *G. serrulata* fertile laminae are often (but not always) strongly conduplicate, thus making the distal portion appear even narrower to the naked eye.

Grammitis subtilis (Kunze ex Kl.) Morton, *Contr. U.S. Natl. Herb.* 38: 104. 1967. *Polypodium subtile* Kunze ex Kl. *Linnaea* 20: 375. 1847.
Ctenopteris subtilis (Kunze ex Kl.) J. Sm. *Hist. Fil.* 184. 1875.

A rare fern, in forests or wooded ravines, on tree trunks, rock walls, or ravine banks, 1,200-1,500 m.; Alta Verapaz; Baja Verapaz. Costa Rica; Panama; Colombia; Venezuela; Ecuador.

Rhizome erect, compact, provided with blackish (or deep-castaneous), nonclathrate scales, these 0.3-0.8 mm. long, ovate to lanceolate, sparsely setose, the setae rigid, whitish, often somewhat deciduous; leaves subfasciculate, 3-10 (-12) cm. long, 0.5-1 cm. broad, very short-petiolate; petiole 0.4-1 cm. long, 0.2-0.3 mm. thick, terete, gray-brown to blackish, copiously provided with long, silky, spreading, unicellular trichomes, these orange or tawny, 1-2 mm. long; lamina thin-herbaceous, linear to narrow-elliptic or -lanceolate, pinnate, tapering gradually at both ends; rachis blackish, amply pilose as on the petiole; pinnae numerous, larger ones 2-5 mm. long, 1-2 mm. broad, spreading to

slightly ascending, adnate, oblong, obtuse, the margins entire, plane, the acroscopic margin commonly perpendicular to the rachis, the basiscope slightly decurrent, abundantly pilose, with simple trichomes, as on the axis, the trichomes 1.5-2.5 mm. long; costa indistinct to obscure; veins obscure, simple, 2-5, short (some of them merely spurs), the tips somewhat dilated into hydathodes, these adaxially bearing conspicuous, white, circular, calcareous scales; sori discrete, round, inframedial, borne at vein tips, not impressed in the tissue, (1) 2-5 on each pinna; sporangia glabrous.

In Morton's key to the genus in Ecuador (1967), he lists *G. subtilis* with the species having setose sporangia. Copeland (Phillip. J. Sci. 84: 399. 1956) stated that sporangia are "apparently naked." In closely scrutinizing specimens throughout the range, I have observed that the sporangia are without setae or trichomes of any kind. With this perhaps should be included *Polypodium cretatum* Maxon of Jamaica, which apparently differs only in its darker trichomes.

Grammitis trichomanoides (Sw.) Ching, Bull. Fan. Mem. Inst. Biol. Bot. 10: 16. 1940. *Polypodium trichomanoides* Sw. Nov. Gen. Sp. Pl. Prodr. 1788. *Ctenopteris trichomanoides* J. Sm. Hist. Fil. 184. 1875. *Xiphopteris trichomanoides* (Sw.) Copel. Gen. Fil. 215. 1947.

On trunks and branches of trees, 1,350-1,700 m.; Alta Verapaz; Baja Verapaz; Chiquimula. Honduras; Jamaica; Cuba; Hispaniola; Colombia; Venezuela; (French Guiana?).

Rhizome rather stout, erect or ascending, provided with lanceolate, subclathrate scales, these 2-4 mm. long, yellowish to orange, with margins remotely and irregularly toothed, to subentire; leaves 5-12 cm. long, 0.4-0.8 cm. broad, sessile or very short-petiolate; petiole often lacking, or rarely to 1 cm. long; lamina linear or linear-elliptic, tapering gradually at both ends, decurrent at base, cut nearly to the rachis, abundantly provided with spreading, castaneous, unicellular trichomes, these 1-2 mm. long; segments numerous, most of them narrowly oblong, 2-2.5 times as long as broad, spreading at a broad (usually 90°) angle from the rachis, usually with subparallel sides, but often gibbous at the base acroscopically, the proximal segments strongly and gradually shortened, thus the lowermost becoming broader than long; veins obscure, mostly 1-forked, the branch strongly produced, both tip and branch terminating in a distinct hydathode; sori round, discrete, one to a segment, borne on the vein branch; sporangia glabrous.

This scarcely differs from *G. cookii*, under which see further discussion.

GYMNOPTERIS Bernhardt

REFERENCES: L. M. Underwood, Amer. ferns IV, The genus *Gymnogramme* of the Synopsis Filicum, Bull. Torrey Bot. Club 29: 617-634. 1902. W. R. Maxon, Studies of tropical American ferns No. 6, Contr. U.S. Natl. Herb. 17: 541-608. 1916. D. B. Lellinger, The taxonomic position of *Coniogramme americana*, Amer. Fern J. 59: 61-65. 1969.

Plants of small to medium size, terrestrial; rhizome erect to short-creeping, scaly; leaves essentially monomorphic, erect; petiole at least sparsely pubescent with septate trichomes and sometimes scaly, not articulate; lamina firm-herbaceous to subcoriaceous, pinnate to (less commonly) 2-pinnate, with a conform or subconform apical segment, not or scarcely reduced at base; rachis glabrous to abundantly pubescent with septate trichomes; pinnae few to a dozen pairs, commonly well spaced, acute or subacute, adnate to short-stalked; venation free to (in *G. subcordata*) partially areolate, the veins commonly forked; sporangia short-stalked, borne abaxially along the veins, not confluent, or occasionally becoming crowded and subconfluent in some mature plants; indusia and paraphyses lacking; spores trilete, tetrahedral-globose, variously ornamented, with perine.

Gymnopteris is very closely related to the genus *Hemionitis* L. In fact, there is good evidence to indicate the two might be better combined. A fine paper by Mickel (Amer. Fern J. 64: 3-12. 1974) compares the traditional "differences" of these two taxa and points out how few of them are consistent and/or significant. Of all the features, only that of lamina configuration seems to hold up. It is thus obvious that more research is needed before generic boundaries can be properly delimited. Nevertheless, pending further study, *Gymnopteris* is tentatively treated in our Flora as distinct, on the strength of its pinnate to 2-pinnate (*vs. Hemionitis*' pinnatifid to palmate) lamina.

Gymnopteris is also related to the Old World genus *Coniogramme* Fée. Indeed, one of our species, *G. subcordata*, has been for some time treated as *C. americana*. However, Lellinger (1969) has shown that its proper position is within *Gymnopteris*.

Circumscribed as above, the genus contains 6-7 species scattered throughout the tropics of both hemispheres, two of which occur in Guatemala.

- a. Venation free; petiole castaneous to atropurpureous, abundantly pilose with septate trichomes, and densely puberulous with minute acicular ones; most pinnae short-stalked, the stalks castaneous, the dark color ending abruptly at the pinna base. *G. rufa*.
- a. Venation partially areolate, commonly many (but at least a few) areoles present between costa and margin; petiole stramineous, sparsely pilose with septate trichomes or glabrate; most pinnae adnate, the stalks (if any) stramineous to gray-brown, their color extending well up into the pinnae. *G. subcordata*.

***Gymnopteris rufa* (L.) Underw.** Bull. Torrey Bot. Club 29: 627. 1902. *Acrostichum rufum* L. Syst. Nat. ed. X. 2: 1320. 1759 (not *Pteris ruffa* L. 1753). *Gymnogramma rufa* (L.) Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 304. 1811.

In forests, thickets, or partly open areas, sometimes along river banks, 50-500 m.; Izabal; Petén; Retalhuleu. Southern Mexico to

Panama; Cuba; Jamaica; Colombia to Surinam, south to Brazil and Peru.

Rhizome small, erect, provided at apex with linear, attenuate scales, these 3-5 mm. long, entire, orange or with a narrow, lustrous dark-brown to blackish median stripe; leaves several, caespitose, to 75 cm. long and 14 cm. broad; petiole stout, 2-4 mm. in diameter, 20-40 cm. long, about as long as the lamina, castaneous to atropurpureous, somewhat lustrous, terete, amply provided at base with orange, linear scales as on the rhizome and densely covered throughout with spreading, orange, septate trichomes 2-3 mm. long and amply to densely puberulous with very minute, apparently 1-celled trichomes; lamina 1-pinnate, chartaceous, narrow-elliptic or -lanceolate, margins and both surfaces amply pilose with orange, septate trichomes, scarcely reduced at base, terminating abruptly in a conform or subconform (occasionally hastate) apical segment; rachis castaneous, densely provided as on the petiole with both long, spreading, septate trichomes, and minute, 1-celled, acicular ones; pinnae 6-12 pairs, commonly spreading at a 90° angle with the rachis, subdistant, lanceolate, entire, acute at apex, all but the distal ones short-stalked, the stalks castaneous, the dark color ending abruptly at the truncate, broadly cuneate or (rarely) subcordate base (or sometimes a few proximal pinnae auriculate or hastate); veins free, spreading obliquely from the costa, 1- or 2-forked, terminating well short of the margin.

Gymnopteris subcordata (Davenp. in Rose) Underw. Bull. Torrey Bot. Club 29: 628. 1902. *Gymnogramme subcordata* Davenp. in Rose, Contr. U.S. Natl. Herb. 5: 138. 1897. *Coniogramme subcordata* (Davenp. in Rose) Maxon, *op. cit.* 17: 174. 1913. *nom. illeg.* (not Copel. 1910). *C. americana* Maxon, *tom. cit.* 607. 1916.

Apparently represented in Guatemala from a single collection: In valley along river, alt. 700-800 m., along Río Nentón, just west of Nentón, Sierra de los Cuchumatanes, Dept. Huehuetenango (*Steyermark 51433*). Elsewhere found in forests and shaded ravines, as well as on grassy, open slopes, 20-800 m. Mexico; Honduras; Nicaragua; Costa Rica.

Rhizome stout, short-creeping to suberect, amply provided with linear, attenuate scales, these 2-3 mm. long, entire, orange to dark brown or blackish or orange with a blackish, median stripe; leaves crowded or contiguous, to 60 cm. long and 17 cm. broad; petiole wiry, 1-3 mm. in diameter, 12-30 cm. long, 1-2 times as long as the lamina (rarely shorter), stramineous, or light brown at base, flattened or obtusely angled, sulcate adaxially, sparsely provided with orange, linear scales or septate trichomes, or glabrate; lamina pinnate to pinnate-pinnatifid, occasionally ternate, firm-herbaceous to chartaceous, deltoid- to elliptic-ovate, abruptly terminating in a conform apical segment, surfaces glabrous, or the abaxial side sparsely scaly or pubescent, the trichomes or filamentous scales (when present) scattered, minute, and usually appressed; rachis stramineous, glabrous, or sparsely provided with orange, spreading, septate trichomes; pinnae 1-7 pairs, weakly ascending, subdistant, lanceolate or ovate, acute to subacute at apex, entire to deeply pinnatifid (or rarely a few basal ones quite to the costa), adnate, or the proximal ones short-stalked, the stalks stramineous to gray-brown, the color extending well into the cuneate, truncate, or subcordate (often inequilateral) base; veins predominantly free, but a few to (commonly) many merging to form elongated areoles, the ultimate branches running free and fully to the pinna or segment margin.



FIG. 34. *Gymnopteris*. **a-b**, *G. rufa*: a, habit, $\times \frac{1}{2}$; b, base of fertile pinna, $\times 6$; **c-d**, *G. subcordata*: c, base of fertile pinna, $\times 6$; d, base of sterile pinna and veins, $\times 6$.

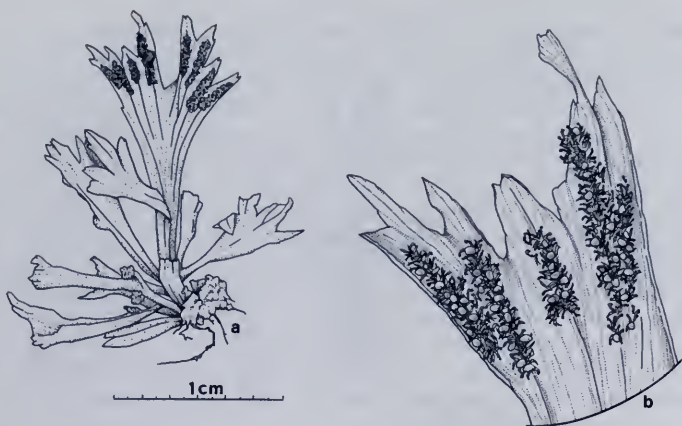


FIG. 35. *Hecistopteris pumila*. a, habit, $\times 3$; b, leaf apex with sporangia and paraphyses.

HECISTOPTERIS John Smith

Plants diminutive, epiphytic; rhizome filiform, creeping, scaly only at the base of leaves, the scales linear, clathrate, lustrous, dark brown, 1 mm. long or less; leaves caespitose, monomorphic, sessile or subsessile, 1-3 cm. long, 0.2-0.6 cm. broad; lamina thin-herbaceous, glabrous, cuneiform to subflabellate, the margins entire, the apex deeply dentate to irregularly and sharply cleft; veins free, indistinct or obscure, subdichotomously forked, a strong midrib lacking; sori linear, borne abaxially along the veins or vein branches, mostly distal on the lamina, but not extending to the apex; paraphyses brown, filiform, often numerous; indusium lacking; spores trilete, tetrahedral, probably without perine.

The genus contains but a single species, and is confined to the neotropics. On herbarium labels it is usually described as "rare," and perhaps this is true; but its range includes most of the West Indies and Central and South America, and I would presume a more proper description would be "rarely collected." This is one of the tiniest of all ferns, and it may be supposed that hundreds of collectors have passed within arm's length of the plant without observing it.

Hecistopteris pumila (Sprengel) J. Sm. J. Bot. (London) 1: 193. 1842. *Gymnogramma pumila* Sprengel, Tent. Suppl. Syst. Veg. 31: 1828.

In wet forests, on tree trunks, sea level to 100 m.; Alta Verapaz;

Izabal. West Indies; British Honduras to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Characters are those of the genus.

HEMIDICTYUM Presl

Plants large, terrestrial, erect; rhizome stout, erect, provided with broad, brown, clathrate scales; leaves several, fasciculate, monomorphic, petiolate, to 2 m. long and 0.8 m. broad; petiole stout, subterete, to 1 m. long, sparsely scaly near the base, not articulate; lamina glabrous, drying thin-herbaceous, simply pinnate, somewhat reduced at base, the apical segment similar in size and shape to the pinnae; rachis smooth, glabrous, rounded abaxially, sulcate adaxially; pinnae narrow-oblong, to 50 cm. long and 12 cm. broad, opposite, remote, sessile, cordate-clasping, short-acuminate, the margin subentire and scarious; veins parallel, approximate, simple or 1-forked, freely anastomosing halfway to the margin, then terminating at an intramarginal vein; sori linear, parallel, borne between the margin and the first areoles; indusium linear, entire, attached to the vein and opening toward the acroscopic side, pale green, drying yellowish brown; sporangia numerous, long-stalked; paraphyses lacking; spores monolet, bilateral, ovoid, with folded perine.

The genus is closely related to *Athyrium* and *Diplazium*. The most outstanding features are the remote, opposite pinnae with cordate-clasping bases and subcontinuous, intramarginal veins, and the close, parallel veins which begin to anastomose about halfway to the margin.

Hemidictyum contains but one species, although *Asplenium purdieanum* Hook. of Colombia and Venezuela has been included in the genus by various authors. However, a clear relationship has not yet been established, and for purposes of this treatment, *Hemidictyum* is considered to be monotypic.

***Hemidictyum marginatum* (L.) Presl, Tent. Pterid. 111. 1836.** *Asplenium marginatum* L. Sp. Pl. 1082. 1753. *A. limbatum* Willd. Sp. Pl. 5: 310. 1810. *Hemidictyum limbatum* (Willd.) Presl, Epim. Bot. 74. 1851. *Diplazium marginatum* (L.) Diels in Engl. & Prantl, Pflanzenf. 1 (4): 229. 1899 (not Blume, 1828).

In dense, wet forests, often along streams, 80-1,000 m.; Alta Verapaz. Southern Mexico to Panama; West Indies; Trinidad & Tobago; Colombia; Venezuela; Brazil; Ecuador; Peru.

Characters are those of the genus.

HEMIONITIS Linnaeus

REFERENCE: J. T. Mickel, A redefinition of the genus *Hemionitis*, Amer. Fern J. 64: 3-12. 1974.



FIG. 36. *Hemidictyum marginatum*. a, leaf apex, $\times \frac{1}{2}$; b, portion of pinna, abaxial surface, $\times 2\frac{1}{2}$; c, portion of pinna, adaxial side, showing lateral veins and intramarginal vein, $\times 6$.

Plants small, terrestrial or epipetric; rhizome short, erect to ascending, scaly, the scales broad to filamentous, rigid to lax; leaves monomorphic or somewhat dimorphic (the sterile leaves commonly shorter and the lamina smaller), crowded to subcaespitose; petiole long, not articulate, sparsely to amply pubescent, lustrous, atropurpureous, the dark color (at least in ours) abaxially passing well into the midribs of lamina and lobes; lamina pubescent, firm-herbaceous to chartaceous, commonly much shorter than the petiole, hastate, sagittate, circular-cordate, palmate or pinnatifid, frequently bearing proliferous buds in the sinuses of adjacent segments; venation areolate, without free included veinlets; sporangia short-stalked, borne abaxially along the veins throughout the lamina, not arranged in discrete sori; indusia and paraphyses lacking; spores trilete, globose-tetrahedral, rather sharply sculptured, with perine.

Hemionitis is closely related to, and may even be congeneric with *Gymnopteris* (under which see further discussion) and *Bommeria*. *Bommeria pedata* (the only Guatemalan species) has free venation, whereas the veins in *Hemionitis* are copiously reticulate. However most other species in *Bommeria* have reticulate venation, so this character is ineffective in a broader scope. Degree of dissection of lamina and proportion of laminar surface covered by sporangia serve to delineate species superficially but hardly can be treated as important generic features. It is clear that further research such as that of Mickel (1974) could show that *Bommeria*, as well as *Gymnopteris*, may be better lumped with *Hemionitis*.

The genus contains 6-8 species, all from the neotropics except one, *H. arifolia*, from southeast Asia. The following have been found in Guatemala.

- a. Lamina palmate, the dark midribs of apical and lateral lobes all diverging from the same point at the base of the lamina. *H. palmata*.
- a. Lamina pinnatifid, consisting of an apical and 2 (3) pairs of lateral segments, the dark midrib (rachis) pinnately branched. *H. pinnatifida*.

***Hemionitis palmata* L. Sp. Pl. 1077. 1753. *Gymnogramme palmata* (L.) Link, Hort. Reg. Bot. Berol. 2: 48. 1833 (not Baker, 1868).**

In moist soil of forests, thickets, and wooded ravines, occasionally (in Guatemala) to frequently on mossy rocks or rocky slopes, 70-900 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Huehuetenango; Izabal; Petén; San Marcos. Mexico to Panama; West Indies; Colombia to the Guianas, south to Bolivia and Brazil.

Plants terrestrial to (less commonly) epipetric; rhizome provided with thin, lax, orange scales, these linear to lanceolate, 2-5 mm. long, often intermixed with orange, pluricellular trichomes; leaves 10-40 cm. long or the sterile ones shorter (6-18 cm.); petiole 7-30 cm. long (those of sterile leaves 3-10 cm.), sparsely to amply provided with spreading, articulate, pluricellular trichomes to 1.5 mm. long; lamina 4-10 cm. long and as broad or broader (sterile ones somewhat smaller), pentagonal, palmately divided, the

segments with margins commonly deep-crenate and apices acute (or less so or obtuse on younger or sterile leaves), amply pubescent on surfaces, veins, and margin, the trichomes like those of the petiole, but less abundant, more rigid, and appressed on the adaxial surface; the tissue opaque and the veins indistinct to obscure, but abaxially the midribs lustrous, atropurpureous, and quite distinct well into each of the 5 segments.

In Guatemala, *H. palmata* is commonly found growing in soil. Only occasionally has it been reported from rocky habitats. However, elsewhere in Central America, and in the West Indies, it is frequently found on very rocky slopes or on mossy rocks or in the crevices of rocky cliffs.

This and *H. pinnatifida* are quite closely related. See treatment of the latter for further discussion.

Hemionitis pinnatifida Bak. in Hook. & Bak. Syn. Fil. 399. 1868.
Gymnogramme pinnatifida Salom. Nomencl. Gefässkrypt. 186. 1883.

In forests and wooded ravines, on moist or dry banks, rarely (in Guatemala) to frequently on rocks or rocky cliffs, 220-1,300 m.; Baja Verapaz; Guatemala; Huehuetenango; Jalapa; Jutiapa; Quezaltenango; Santa Rosa; Zacapa. Southern Mexico; Honduras; El Salvador; Nicaragua.

Plants terrestrial or (rarely in Guatemala) epipetric; rhizome provided with thin, lax, orange to light-brown scales, these linear to lanceolate, 2-5 mm. long, sometimes in age developing dark-brown, sclerotic median stripes, the scales often intermixed with orange, pluricellular trichomes; leaves 8-28 cm. long or the sterile ones shorter (3-8 cm.); petiole 4-24 cm. long (those of sterile leaves 1-4 cm.), amply to densely provided with spreading, articulated, pluricellular trichomes to 1.5 mm. long; lamina 4-10 cm. long and about as broad (sterile ones somewhat smaller), deeply pinnatifid, deltoid to subpentagonal, with an apical segment and 2-3 pairs of lateral ones, amply to abundantly pubescent on surfaces, veins, and margins, the trichomes like those of the petiole, but less abundant, more rigid and appressed on the adaxial surface; segments subentire to deeply crenate, acute or subacute (or less so or obtuse on younger or sterile leaves), the basal pair commonly provided with large, basiscopic lobes, these often nearly as large as the distal segments; the tissue opaque and the veins indistinct to obscure, but abaxially the rachis and midribs of segments and lobes lustrous, atropurpureous and quite distinct for much of their length.

This species differs little from *H. palmata*, except in the lamina architecture, as noted in the key. The leaves are not generally as long as those of the latter, especially the sterile ones, so that these often form a nearly sessile rosette. The petiole and lamina in *H. pinnatifida* seem to be usually more abundantly pubescent, and the rhizome scales tend to have their centers rather commonly darkened and sclerotic. I have not observed this condition in any of the Guatemalan specimens of *H. palmata*.



FIG. 37. *Hemionitis*. a-b, *H. palmata*: a, habit, $\times \frac{1}{2}$; b, portion of lamina, showing sporangia and proliferous bud; c, *H. pinnatifida*, lamina, $\times \frac{1}{2}$.

HISTIOPTERIS (J. G. Agardh) J. Smith

Plants terrestrial; rhizome slender, long-creeping, scaly, and often pubescent; leaves usually quite large, essentially monomorphic, petiolate, glabrous, or sparsely pubescent with septate trichomes along the axes abaxially; petiole not articulate, glabrous or very sparsely pubescent and/or scaly at base; lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatifid, firm-herbaceous to subcoriaceous; pinnae short-stalked, sessile, opposite or subopposite, spreading at right angles from the rachis, or ascending; ultimate segments commonly sessile, opposite or subopposite; venation copiously to (in ours) partially areolate; sori commonly elongated, borne on a marginal commissure which connects the vein tips; indusium marginal, commonly elongated, flaplike, opening inward, composed of a slightly to greatly modified, reflexed portion of the segment margin; paraphyses ample to abundant, light brown to castaneous; sporangia stalked, borne in a line along the marginal commissure; spores monolete, bilateral, lacking perine.

Histiopteris is a small, pantropical genus, with seven (or probably less) Old World and one American species. Its affinities are with *Lonchitis*, *Pteris*, and perhaps *Hypolepis*.

***Histiopteris incisa* (Thunb.) J. Sm. Hist. Fil. 295. 1875. *Pteris incisa* Thunb. Prodr. Pl. Capens. 171. 1800.**

In forests, thickets, and wooded ravines, also in meadows and on open slopes, 1,500-3,100 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Quezaltenango; El Quiché. West Indies; southern Mexico to Panama; Colombia and Venezuela, south to Brazil and Bolivia; Juan Fernandez Islands; Old World tropics.

Rhizomes amply provided with amber to castaneous, lustrous, clathrate scales, these to 2 mm. long, linear, attenuate, the tips commonly septate, composed of a single row of cells, the scales often intermixed with minute, filiform trichomes, these rigid, amber, to 1 mm. long; leaves erect, larger ones often clambering over shrubs, 0.5-2 m. long; petiole shorter than the lamina, terete abaxially, shallow-sulcate adaxially, yellowish brown to castaneous, or atropurpureous at base, glabrous or sparsely pubescent and/or scaly at base, often somewhat glaucous; lamina broadly oblong or ovate, scarcely or not reduced at base, tapering to a pinnatifid apex, essentially glabrous, often glaucous abaxially; pinnae sessile, with basal pinnules commonly overlapping the rachis, crowded or imbricate to sometimes widely spaced; ultimate segments obtuse to acute, entire to deeply lobed; venation partially areolate, *i.e.*, the veins mostly free and several times forked, but the basal forks of adjacent veins commonly joining to form areoles along the midrib or costule, the free vein tips not or scarcely enlarged, terminating at the margin of the segment; sori short to greatly elongated, marginal, commonly ending short of the segment tip and the sinus (on smaller lobes occasionally extending fully around the sinus); indusia either a single one running along the margin for nearly the length of each ultimate segment, or 2-5 shorter ones, close to widely separated, thick-textured and whitish, or thin and scarious, subentire to erose.

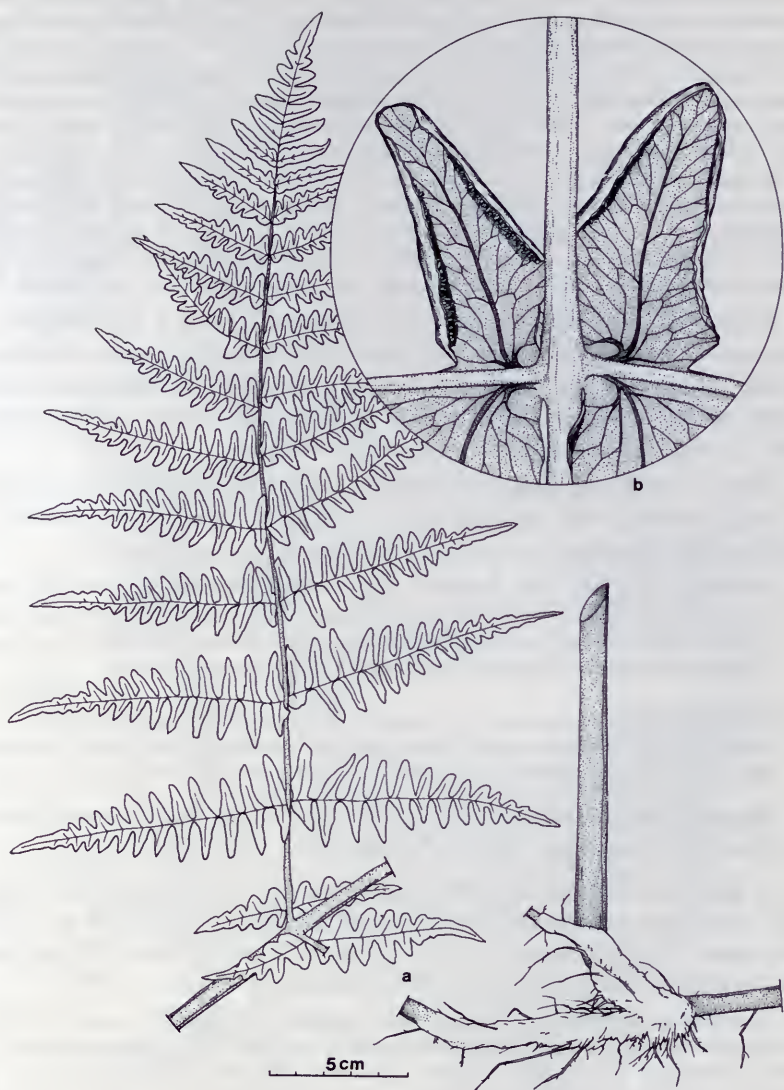


FIG. 38. *Histiopteris incisa*. a, rhizome and a central pinna, $\times \frac{1}{2}$; b, rachis and bases of pinnae, $\times 3$.

HYPOLEPIS Bernhardt

Plants terrestrial, erect to scandent; rhizome long-creeping, lacking scales, but sparsely to amply pubescent, the trichomes articulated, often moniliform; leaves large, monomorphic, pubescent to glabrous, lacking scales; petiole not articulate, commonly quite long, this and the axes often short-spiny; lamina 2-pinnate to 4-pinnate-pinnatifid, herbaceous to chartaceous, broad, ovate to subdeltoid, tapering gradually to a pinnatifid apex; pinnae (at least in ours) greatly dissected, spreading (often at a 90° angle); veins free, forked to pinnately branched in each ultimate segment, the branch tips terminating at or near the margin; sori terminal on the vein branches abaxially, borne (at least in ours) at the tip of the basal acroscopic branch, at or near the sinus formed by 2 adjacent segments; indusium (or pseudindusium) consisting of a slightly to strongly modified lobe of the segment, the lobe not at all to strongly reflexed and protecting the sorus; paraphyses lacking; sporangia stalked; spores monolete, planoconvex, with perine.

Hypolepis is closely related to *Dennstaedtia*, and a few species of each could be easily confused. However, the indusium in *Dennstaedtia* is commonly cup-shaped, formed by a true, inner indusium partially fused with a (somewhat to scarcely) modified lobe of the segment margin. In *Hypolepis* the inner indusium is lacking.

This is a pantropic genus containing 40-50, often ill-defined, species. A good revision will perhaps place a dozen of these into synonymy. Two readily distinguished species are found in Guatemala.

- a. Penultimate segments inequilateral at base, cuneate basiscopically, truncate and more strongly produced acroscopically, bearing no more than 5 (6) pairs of segments or lobes; costae adaxially sulcate, the marginal ridges raised and continuous as ridges or herbaceous wings along the axes of the next order above or below.

H. nigrescens.

- a. Penultimate segments equilateral at base, at least the largest ones bearing 7-15 pairs of segments or lobes; costae not or faintly grooved adaxially, lacking raised, marginal ridges which are continuous onto axes of the next order above or below. . *H. repens.*

***Hypolepis nigrescens* Hook. Sp. Fil. 2: 66, t. 90. 1852. *Dennstaedtia rubicaulis* Christ, Bull. Herb. Boissier II. 4: 258. 732. 1905.**

In forests or in clearings, often scandent and spreading over shrubs and low trees, sometimes forming small thickets, 1,100-2,300 m.; Alta Verapaz; Huehuetenango; El Progreso. Southern Mexico; Honduras; El Salvador; Costa Rica; Colombia; Venezuela; Brazil.

Plants terrestrial; leaves to 5 m. long; petiole stout, to 1.5 cm. thick, amply to abundantly provided with sharp, stout spines (these to nearly 1 mm. long) and sparsely to amply pubescent with minute, reddish, appressed, articulated trichomes; lamina 3-pinnate to 4-pinnate-pinnatifid, firm-herbaceous, tissue between the veins glabrous; rachis stramineous to light brown, aculeate and pubescent as on the petiole, terete abaxially, sulcate adaxially; pinnae numerous, short-stalked, spreading from the rachis at right angles, or slightly ascending; costa sparsely to amply aculeate and pubescent, abaxially terete, adaxially sulcate, with wings of green tissue or marginal ridges continuous as ridges along the axes of the next order above and below; penultimate seg-



FIG. 39. *Hypolepis*. a-b, *H. repens*: a, rhizome and a central pinna, $\times \frac{1}{2}$; b, base of pinnule, abaxial surface, $\times 6\frac{1}{2}$; c-d, *H. nigrescens*: c, base of pinnule, abaxial surface, $\times 3\frac{1}{2}$; d, costa and bases of pinnules, adaxial side, $\times 3\frac{1}{2}$.

ments inequilateral at base, cuneate basiscopically, truncate and more strongly produced acroscopically, each bearing 3-5 (6) pairs of segments or lobes; ultimate segments or lobes adnate, obovate, dentate, sparsely pubescent along the veins, or glabrate; veins pinnately arranged, the tips of branches terminating at the segment margin; sori borne singly on the tip of the basal acroscopic vein, at the sinus between 2 segments or lobes; indusium formed by a somewhat modified lobe of tissue, drying whitish to yellowish or dark brown, margin entire to erose, or ciliate (the cilia commonly deciduous at maturity).

Hypolepis repens (L.) Presl, Tent. Pterid. 162. 1836. *Lonchitis repens* L. Sp. Pl. 1078. 1753. *Cheilanthes repens* (L.) Kaulf. Enum. Fil. 215. 1824.

In secondary forests, thickets, and wooded ravines, often spreading over shrubs, 80-2,300 m.; Alta Verapaz; Baja Verapaz; Quezaltenango. Southern Mexico to Bolivia and Brazil; West Indies; Florida.

Plants terrestrial; leaves to 6 m. long; petiole stout, sparsely to amply provided with sharp, stout spines to 1 mm. long, glabrate, or sparsely pubescent with minute, reddish, commonly appressed, articulated trichomes; lamina 3-pinnate to 4-pinnate-pinnatifid, firm-herbaceous to chartaceous, sparsely to amply pubescent on and between the veins, or glabrate; rachis stramineous to light brown, aculeate and pubescent as on the petiole, terete to subquadrangular, not or faintly grooved adaxially; pinnae numerous, short-stalked, spreading from the rachis at broad (often 90°) angles from the rachis; costa sparsely to amply aculeate and pubescent, terete to subquadrangular, not or faintly grooved adaxially, lacking raised, marginal ridges which are continuous onto axes of the next order above or below; penultimate segments equilateral at base, each bearing (5) 6-15 pairs of segments or lobes; ultimate segments or lobes broadly oblong, subentire or crenulate, minutely pubescent between and/or on the veins, or glabrate; veins several-forked to pinnately arranged, the tips of branches terminating near the segment margin, these often somewhat swollen adaxially; sori borne singly on the tip of the basal acroscopic vein, at the sinus between 2 segments or lobes; indusium (or pseudindusium) formed by a slightly to strongly modified lobe of tissue, drying whitish, greenish, or yellow-brown, the margin subentire to erose.

With this might perhaps be included several other species from Central or South America, such as *H. mexicana* Liebm. and *H. hostilis* (Kze.) Presl. A number of neotropical taxa are ill-defined species supposedly differing from *H. repens* in size of ultimate segments, ciliate indusia margins or abundance of spines and pubescence. Further study is needed to clarify relationships.

JAMESONIA Hooker & Greville

REFERENCES: A. F. Tryon, A monograph of the genus *Jamesonia*, Contr. Gray Herb. 191: 109-197. 1962.

Plants of small to medium size, terrestrial, occurring at medium to very high altitudes; rhizome slender, creeping, lacking scales, but provided with short, rather stout and rigid

trichomes; leaves monomorphic, linear, indeterminate or sometimes (outside Guatemala) determinate, variously beset with trichomes, but lacking scales; petiole not articulate, commonly much shorter than the lamina, this and the rachis terete to obtusely angled, often sulcate adaxially, moderately to densely tomentose; lamina 1-pinnate, herbaceous to (in ours) coriaceous, moderately to densely tomentose (at least abaxially); pinnae numerous, mostly imbricate and in 2 ranks, suborbicular (in ours) to obtusely ovate, with margins somewhat to strongly revolute; veins free, dichotomous; sporangia stalked, borne abaxially on the veins, in some species (ours included) often so numerous as to obscure the abaxial surface of pinnae; paraphyses commonly lacking; indusia lacking, but the inrolled margins of pinnae often serving to protect the maturing sporangia; spores trilete, globose-tetrahedral, perine lacking.

Jamesonia is among the most distinctive genera of ferns. The linear shape of the leaves and the usually small, orbicular, imbricate pinnae are not likely to be confused with those of any other ferns. Although some of its species thrive in forested, protected areas, most are well adapted for survival in areas on the high paramos where there is great exposure to wind, sun, and cold. Unless one is familiar with the genus, it can be often rather difficult to distinguish between many of the species, so with some critical characters it is necessary to examine the plants under high magnification. Alice Tryon's monograph (1962) is an excellent piece of work which has cleared up most of the problems in this difficult genus. She recognizes 19 species, occurring from Southern Mexico to Bolivia and Brazil, only one of which is found in Guatemala.

***Jamesonia alstonii* A. F. Tryon, Contr. Gray Herb. 191: 168. 1962.**

On the tops and upper slopes of mountains, in cloud forests or in exposed locations above tree line, among rocks or in rock crevices, 2,900-4,200 m.; Huehuetenango; San Marcos. Southern Mexico (Chiapas); Nicaragua; Costa Rica; Colombia to Bolivia.

Plants terrestrial or epipetric; rhizome short- to long-creeping, provided with rigid, appressed trichomes, these commonly dark brown or blackish, lustrous, 1.5-2.5 mm. long; leaves subdistant to densely crowded, 20-45 cm. long; petiole 2-5 cm. long, often strongly bent, terete, lustrous, atropurpureous, amply pubescent, the trichomes proximally much like those of the rhizome, but distally becoming lighter brown, flexuous, and spreading; lamina 1-pinnate, 0.5-1 cm. broad, coriaceous, linear, about the same width throughout, or slightly reduced toward the base; rachis densely tomentose with light-brown to stramineous, septate trichomes, terete to slightly flattened or angular, atropurpureous; pinnae very numerous, commonly in 2 ranks, 3.5-4.5 mm. long, 2-5 mm. broad, mostly imbricate, but becoming contiguous to subdistant near the lamina base, short-stalked (0.2-0.5 mm.), commonly orbicular-cordate, inequilateral at base, margins revolute, adaxial surface glabrous (sometimes minutely glandular), abaxial surface sparsely provided with short trichomes, these with short, bulbous terminal cells; veins distinct to indistinct, commonly once-branching at a broad angle, the branch tips terminating short of the pinna margin; sporangia abundant, commonly covering the abaxial surface of the pinna, with short to moderately long stalks.

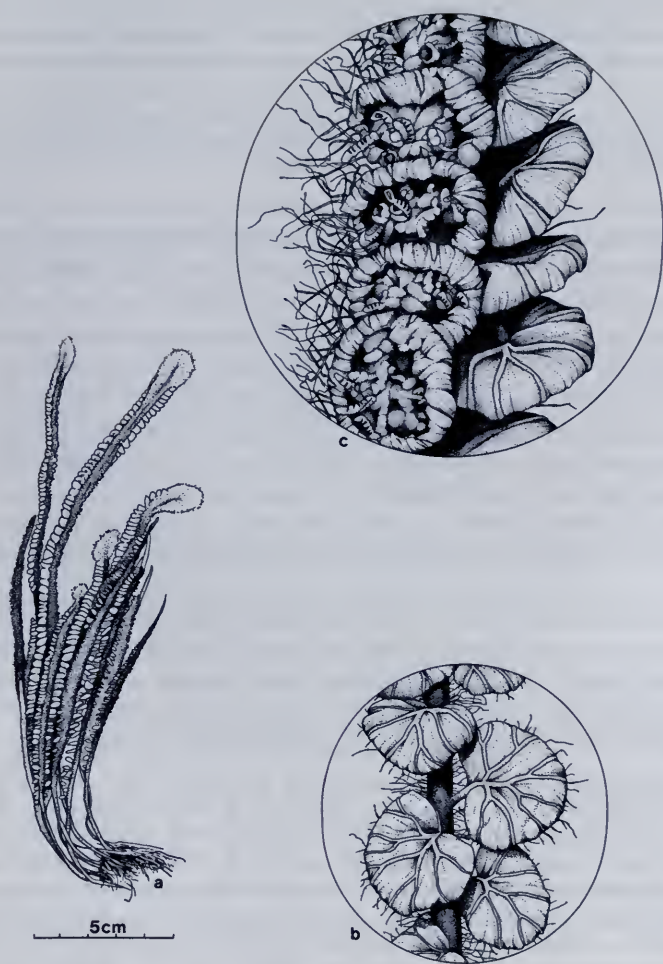


FIG. 40. *Jamesonia alstonii*. a, habit, $\times \frac{1}{2}$; b, portion of rachis and pinnae, adaxial side, $\times 6$; c, several pinnae, abaxial side, $\times 12\frac{1}{2}$.

This is most closely related to the Andean *A. goudotii* (Hieron.) C. Chr., the latter differing especially in the bicolorous tomentum of the apex and rachis, and in the lamina which is much broader distally than proximally.

LASTREOPSIS Ching

REFERENCES: Carl Christensen, Subgenus X, *Parapolystichum* (pp. 93-101) in: A monograph of the genus *Dryopteris*, Part II . . . Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII (6): 1-132. 1920. Mary D. Tindale, A monograph of the genus *Lastreopsis* Ching, Contr. New So. Wales Natl. Herb. 3: 249-339. 1965.

Plants terrestrial (in ours) or rarely epiphytic; rhizome short-creeping (in ours) or long-creeping to erect, commonly amply provided with brownish scales, these linear to narrow-ovate, subentire or sometimes slightly to strongly denticulate or fimbriate; leaves monomorphous, long-petiolate, approximate to subfasciculate; petiole not articulate, scaly below as on the rhizome, abaxially rounded, toward the apex adaxially bearing 2 raised, parallel ridges, the channel between them commonly provided with short, reddish, septate, pluricellular trichomes (and in a few species also with longer, glandular trichomes); lamina rarely less than 2-pinnate, commonly 3- to 5-pinnate, often glandular abaxially, firm-membranaceous to coriaceous, broadly deltoid, or pentagonal due to the basiscopically produced basal pinnae, tapering to a pinnatifid apex, in some species bearing a scaly, proliferous bud in the axil of an upper pinna; rachis with parallel ridges on the adaxial side, which are continuous either as ridges on the axis of the next order above or as cartilaginous leaf margins, the channel between being partially raised and densely covered with septate trichomes as on the petiole (rarely glabrous); pinnae greatly dissected, with pinnules catadromous throughout (except anadromous as to the basal pinnae), commonly inequilateral at base, the basal pair with basal basiscopic pinnules much the larger, but in all other pinnae with basal acroscopic pinnules much the larger; venation commonly catadromous (at least at base), only rarely anadromous, veins free, the branches simple or forked, reaching or nearly reaching the segment margin; sori abaxial on the veins, borne (at least in ours) medially on the vein branches; indusium circular-reniform, or lacking; paraphyses lacking; sporangium long-stalked, glabrous, but often with 1 or 2 stalked glands on the pedicel; spores monolete, bilateral, with perine.

Lastreopsis and *Ctenitis* were treated by Christensen in his monograph (1920) as two closely allied subgenera of *Dryopteris*. A significant characteristic shared by both is that of the peculiar "Ctenitis hairs." These are the short, unbranched, pluricellular, septate, usually reddish trichomes which are found, often in great abundance, along the major axes of the lamina. Many other characteristics, including leaf outline and dissection, are so similar in both genera that they are sometimes difficult to separate. However, the configuration of the axes on the adaxial side of the lamina furnishes one of the more positive means of identification. In *Lastreopsis*, there is a pair of parallel,

raised ribs or ridges along the edges of the minor axes which are decurrent as ridges on the axes of the next order below. They are also continuous as thickened margins of the leaf segments above. In *Ctenitis* such ridges are lacking, or if present they are interrupted, and not decurrent onto the axes of the next order above or below.

Lastreopsis consists of about 33 species, which are found in the rain forests of temperate and tropical regions around the world. It is a predominantly Old World genus, with only 5 species occurring in the neotropics. Two subspecies are found in Guatemala.

- a. Indusium circular-reniform, subsistent; tissue and veins on abaxial side amply provided with yellowish to reddish glands (these sometimes falling away in age); lamina gradually tapering to an attenuate apex. . . . *L. exulta* ssp. *guatemalensis*.
- a. Indusium lacking; tissue and veins eglandular (or veins sparsely glandular); lamina rather abruptly narrowing to an acute or subacuminate apex.
L. effusa ssp. *divergens*.

Lastreopsis effusa (Sw.) Tindale, ssp. *divergens* (Willd.) Tindale, Contr. New So. Wales Natl. Herb. 3: 299. 1964. *Polypodium divergens* Willd. in Schkuhr, Kryptog. Gew. 27, t. 26b. 1806. *P. dilatatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V: 208 (seors. 56) 1849. *Phegopteris divergens* (Willd.) Fée, Gen. Fil. 243. 1852. *Dryopteris effusa* (Sw.) Urban var. *divergens* (Willd.) Hieron. Bot. Jahrb. Syst. 34: 447. 1905. *Ctenitis effusa* (Sw.) Copel. var. *divergens* (Willd.) Proctor, Checklist Jam. Pterid. 18. 1953. *Parapolystichum effusum* (Sw.) Abbiotti var. *divergens* (Willd.) Abbiotti, Revista Mus. la Plata, Secc. Bot. 9: 19. 1958. *L. effusa* ssp. *dilatata* (Liebm.) Tindale, Contr. New So. Wales Natl. Herb. 3: 299. 1964.

In wet forests and thickets, often in ravines or on stream banks, 350-1,800 m.; Alta Verapaz; Quezaltenango; San Marcos; Santa Rosa. Mexico; British Honduras; Honduras to Panama; Greater Antilles; Trinidad; British Guiana to Colombia, southward to Bolivia and Brazil.

Plants terrestrial; rhizome stout, short-creeping, provided with rigid, lustrous, orange to dark-brown, lanceolate scales; leaves approximate, to 2 m. long and 0.8 m. broad; petiole 0.5-1 m. long, drying light brown to stramineous (darker at base), smooth, not or slightly lustrous, sulcate adaxially, toward the base provided with linear to lanceolate, attenuate brown scales; lamina 3-pinnate-pinnatifid to (more commonly) 4-pinnate-pinnatifid, firm-membranaceous to chartaceous, deltoid, acute or subacuminate at apex, essentially eglandular, but sometimes very sparsely provided with hairlike glands abaxially along the veins; rachis light brown to stramineous, narrow-alate near the apex, subglabrous to sparsely hirsute abaxially, densely hirsute in the adaxial furrow, often bearing a scaly, proliferous bud in the axil of an upper pinna; pinnae numerous, stalked, crowded or imbricate, the costae narrow-alate nearly to base, amply to densely hirsute on both sides; pinnules stalked, catadromous throughout, except anadromous on the basal pinnae, costules hirsute (densely so adaxially); tertiary segments adnate to a narrowly alate costule, pinnatisect or (more commonly) subpinnate-



FIG. 41. *Lastreopsis*. a-b, *L. exculta* ssp. *guatemalensis*: a, habit, $\times \frac{1}{2}$ (showing long-tapering apex); b, pinna base, abaxial side, $\times 5$; c-e, *L. effusa* ssp. *divergens*: c, silhouette of leaf, $\times \frac{1}{2}$; d, portion of lamina near apex, abaxial side, showing proliferous bud, $\times 6$; e, juncture of rachis and costa, adaxial side, greatly enlarged.

pinnatisect, with the ultimate segments once again pinnatifid, the lobes or serrations often sharply acute; venation anadromous throughout, except catadromous only as to the basal acroscopic pinnules; sori borne midway along the vein branches; indusium lacking.

From ssp. *effusa* this differs in having the ultimate segments eglandular (or rarely sparsely glandular beneath) and the secondary and tertiary axes amply to densely hirsute on both sides. In ssp. *effusa*, which is essentially confined to the Greater Antilles, the segments beneath are commonly provided with orange or reddish, rodlike or hairlike glands (at least along the veins) and the secondary and tertiary axes are nearly or completely glabrous on the abaxial side.

Another Antillean subspecies which has been recognized is ssp. *confinis* (C. Chr.) Tindale. This may be distinguished from both the above by its thicker (chartaceous to subcoriaceous) texture and its less dissected (usually 2-pinnate-pinnatifid) lamina.

A fourth subspecies of *L. effusa* was suggested by Christensen and published by Tindale (1964) as ssp. *dilatata* (Liebm.) Tindale, but it is not recognized for purposes of this Flora. It was said to differ from ssp. *divergens* in that the lamina is more highly dissected. However, I have examined a number of specimens cited by both the above authors, and many of those determined as ssp. *divergens* have the lamina more highly dissected than some of those determined as ssp. *dilatata*. This character has questionable value, especially when unsupported by any other.

***Lastreopsis exulta* (Mett.) Tindale ssp. *guatemalensis* (Bak.) Tindale**, Contr. New So. Wales Natl. Herb. 3: 245. 1963. *Aspidium chontalense* Fourn. Bull. Soc. Bot. France 19: 254. 1872. *Nephrodium guatemalense* Bak. in Hook. & Bak. Syn. Fil. ed. 2: 498. 1874 (type from "Choelum," Guatemala, *Salvin & Godman s.n.* 1862). *Dryopteris guatemalensis* (Bak.) O. Ktze. Rev. Gen. Pl. 2: 812. 1891. *A. guatemalense* (Bak.) Christ, Bull. Herb. Boissier 2: 56. 1906. *D. exulta* var. *guatemalensis* (Bak.) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VIII (1): 96. 1920. *L. guatemalensis* (Bak.) Gomez, Brenesia 8: 50. 1976. *L. chontalensis* (Fourn.) Lell. Proc. Biol. Soc. Wash. 89: 716. 1977.

In wet forests, often along streams or rivers, 50-350 m.; Alta Verapaz; Izabal. Southern Mexico; Honduras to Panama; Colombia and Ecuador.

Plants terrestrial; rhizome short-creeping, provided with rigid, entire, dark-brown, lanceolate scales; leaves approximate, 25-75 cm. long, 10-30 cm. broad; petiole about as long as the lamina, drying light or dark brown, smooth, often lustrous, sulcate adaxially, provided with dark-brown scales which are widely scattered, but more numerous at the base; lamina commonly 3-pinnate-pinnatifid, firm-membranaceous to chartaceous,

narrow-ovate to narrow-deltoid or appearing subpentagonal due to basiscopically produced basal pinnae, gradually tapering to a long-attenuate apex, tissue and veins amply provided on the abaxial side with elongated, lustrous, yellow, orange, or reddish glands (these often hairlike or rodlike on mature leaves or falling away on older ones); rachis light brown to stramineous, narrow-alate in the distal half, densely short-hirsute throughout but especially so in the adaxial furrow, often bearing a scaly, proliferous bud in a pinna axil near the apex; pinnae numerous, stalked, crowded or imbricate, with costae narrow-alate nearly or quite to base, amply to abundantly short-hirsute on both sides; pinnules short-stalked or adnate, catadromous throughout, except anadromous on the basal pinnae; tertiary segments commonly adnate to a narrowly alate costule, deeply and acutely lobed, or serrate, the serrations sharply acute; venation anadromous throughout, except catadromous only as to the basal acroscopic pinnules; sori borne about midway along the vein branches; indusia orbicular-reniform, subpersistent, often slightly glandular.

This differs from ssp. *exculpta* (Venezuela and Colombia) chiefly in its much smaller laminae and pinnules. Pinnules of the latter are 1-2 cm. broad, and mature laminae are over 40 cm. long and 25 cm. broad. Pinnules (other than the enlarged basal basiscopic pair) of ssp. *guatemalensis* are 0.5-1 cm. broad, and the lamina is commonly 15-30 cm. long and 10-15 cm. broad.

LINDSAEA Dryander in J. E. Smith

REFERENCE: K. U. Kramer, A revision of the genus *Lindsaea* in the New World, Acta Bot. Neerl. 6: 97-290. 1957.

Plants terrestrial (in ours) or rarely epiphytic; rhizome slender, creeping or ascending, amply provided with linear to broadly lanceolate scales, these usually lustrous, dark brown, not or obscurely clathrate, often reduced to and intermixed with simple trichomes; leaves small to nearly 1 m. long, essentially monomorphous, short- to long-petiolate; petiole not articulate, glabrous (though sparsely scaly at base), terete to quadrangular, often lustrous, stramineous to blackish, darkest at base; lamina glabrous, pinnate to 2-pinnate (in ours) or very rarely simple or 3-pinnate, thin-herbaceous to subcoriaceous, in 2-pinnate leaves with a conform, pinnalike terminal segment; rachis sulcate adaxially, often quadrangular, with the angles obtuse to acute, or occasionally marginate or even alate; ultimate segments commonly (as in ours) dimidiate, sessile to short-stalked; venation areolate or (in ours) free, although in fertile segments the otherwise free veins united by a vascular commissure, the veins dichotomously forked; sori submarginal, borne on the commissure along the acroscopic margin and often around the segment tip, commonly linear and continuous, occasionally short and discrete, or rarely borne at the apex of a single vein; indusium a thin and narrow flap, attached along the commissure and opening toward the segment margin; paraphyses (at least in ours) lacking; sporangia stalked, the annulus sometimes slightly oblique, but still interrupted by the stalk; spores trilete and tetrahedral, rarely monolete, commonly lacking perine.

Lindsaea is a pantropical genus of over 200 species. Kramer (1957), whose treatment I closely follow here, lists 45 species in the neotropics—a number of these each including several varieties and forms. The few species occurring in Guatemala are rather sparsely rep-

resented, with the exception of *L. lancea* var. *lancea*, which appears to be somewhat common in certain areas of Alta Verapaz and Izabal.

- a. Sori interrupted, most of them separated by incisions of the acroscopic margin, the latter broadly crenate to shallowly lobed. *L. klotzschiana*.
- a. Sori (most of them) continuous along the subentire, acroscopic margin.
- b. Axis of penultimate segments conspicuously alate, at least abaxially.
 - c. Petiole terete, this (near the lamina) and the rachis conspicuously alate adaxially; most pinnae definitely stalked. *L. divaricata*.
 - c. Petiole quadrangular (above the base), this and the rachis nonalate; most pinnae sessile or subsessile. *L. quadrangularis* var. *subalata*.
- b. Axis of penultimate segments nonalate (though sometimes the angles acute and faintly marginate).
- d. Penultimate segments rather abruptly terminating in a large, nearly free, apical segment, the ultimate segments adjacent to it at least $\frac{1}{2}$ as long as the largest, central ones. *L. lancea* var. *lancea*.
- d. Penultimate segments strongly and gradually reduced to an attenuate, or indefinite, apex, the distalmost ultimate segments many times smaller than the central ones.
- e. Larger ultimate segments 1.5-3.2 cm. long, commonly 3-3.5 times as long as broad; leaf tissue thin-herbaceous. *L. arcuata*.
- e. Larger ultimate segments rarely reaching 1.5 cm. in length, commonly 1-2 times as long as broad; leaf tissue firm-herbaceous to subcoriaceous.
- f. Veins distinct; ultimate segments mostly twice as long as broad; rachis quadrangular for most of its length. *L. portoricensis*.
- f. Veins indistinct to obscure; ultimate segments mostly 1-1.5 times as long as broad; rachis mostly terete, or obtusely quadrangular distally [*L. stricta*].
- g. Lamina pinnate to 2-pinnate, pinnae (when present) strongly ascending, at 20-30° angles; ultimate segments subcoriaceous.
L. stricta forma *stricta*.
- g. Lamina 2-pinnate (rarely 3-pinnate), pinnae spreading to weakly ascending, at 40-80° angles; ultimate segments firm-herbaceous to chartaceous. *L. stricta* forma *moritziana*.

Lindsaea arcuata Kunze, Linnaea 9: 86. 1835. *L. horizontalis* Hook. Sp. Fil. 1: 214. 1844. *L. galeottii* Fée, Mém. Fam. Foug. V. (Gen. Fil.): 107. 1850-52. *L. trapeziformis* Dryander var. *arcuata* (Kunze) Bak. Fl. Brasil 1 (2): 355. 1870 (in part). *L. lancea* (L.) Bedd. var. *arcuata* (Kunze) Rosenst. Hedwigia 46: 80. 1906.

In forests, along ridges, and in wooded ravines, 800-1,200 m.; Alta Verapaz. Greater Antilles; southern Mexico to Panama; Colombia; Venezuela; Brazil; Peru.

Plants terrestrial; rhizome creeping, amply provided with lustrous, light- or dark-brown scales, these commonly linear, appressed or spreading, 1-2 mm. long; leaves approximate to crowded, 20-80 cm. long, petiolate; petiole 10-40 cm. long, variable, shorter, to equaling, to longer than the lamina, stramineous to castaneous, terete, or distally becoming obtusely (rarely sharply) quadrangular; lamina thin-herbaceous, pinnate or 2-pinnate, the 2-pinnate ones with 1-5 pairs of pinnae and a conform, pinnalike terminal segment; rachis stramineous to light brown, terete to quadrangular, the angles



FIG. 42. *Lindsaea*. a, *L. lancea* var. *lancea*, habit, $\times \frac{1}{2}$; b, *L. portoricensis*, habit, $\times \frac{1}{4}$; c, *L. arcuata*, ultimate segments, $\times 3$; d, *L. klotzschiana*, ultimate segment, $\times 3$; e, *L. divaricata*, portion of rachis and pinna base, $\times 3$.

obtuse to rather acute (rarely marginate); pinnae (when present) subsessile, lanceolate, ascending (at 30-45° angles), slightly to somewhat reduced at base, reduced strongly but gradually to a small terminal segment; costae stramineous to yellowish brown, terete at or toward the pinna base, otherwise quadrangular, the angles becoming very acute distally; pinnules (or pinnae, in simply pinnate leaves) subsessile, larger ones 1.5-3.2 cm. long, 0.5-0.9 cm. broad, commonly 3-3.5 times as long as broad, becoming gradually and conspicuously reduced toward pinna apex, the acroscopic margin subentire; veins 1- to 2-forked, indistinct to obscure; sori continuous along the acroscopic margin; indusium 0.2-0.3 mm. broad, the margin subentire.

***Lindsaea divaricata* Kl. Linnaea 18: 547. 1844.**

Thus far known in Guatemala from two collections: Izabal; *Bernoulli* 861 and *Bernoulli & Cario* 338 (probably near sea level). Guadeloupe; Panama; Colombia to the Guianas, south to Bolivia and Paraguay.

Plants terrestrial; rhizome creeping, provided with rigid, lustrous, dark-brown scales, these linear to lanceolate, 1-2 mm. long; leaves crowded, 30-80 cm. long, petiolate; petiole 15-45 cm. long, usually about as long as or longer than the lamina, lustrous, terete, but distally becoming flattened to broadly sulcate on the adaxial side, and the angles rather conspicuously alate; lamina thin- to firm-herbaceous, 2-pinnate, with 1-6 pairs of pinnae and a conform, pinnalike terminal segment; rachis light brown to castaneous, terete, adaxially alate, the wings 0.2-0.3 mm. broad, light-colored, conspicuous; pinnae lanceolate, spreading to ascending (at 45-60° angles), short-stalked, somewhat reduced at base, abruptly or gradually reduced at apex, the terminal segment broad and discrete, or indefinite; costae reddish or dark brown, terete toward the base, distally quadrangular, with all the angles conspicuously alate; pinnules sessile or subsessile, larger ones 1.4-2 cm. long, 0.5-0.8 cm. broad, usually 2.5-3 times as long as broad, those near the apex slightly to very strongly reduced, the acroscopic margin subentire; veins commonly 2-forked and distinct; sori continuous along the acroscopic margin; indusium very narrow and inconspicuous, 0.1-0.15 mm. broad, the margin subentire.

***Lindsaea klotzschiana* Moritz ex Ettingsh. Farnkr. Jetzwelt 212, t. 145, f. 1 & 2. 1865. *L. klotzschiana* Mortiz, Bot. Zeit. 12: 855. 1854. *nom. nud.* *L. feei* C. Chr. Index Fil. 393. 1906. *L. quadrangularis* auct. (not Raddi, 1819).**

Rare, in forests, 500-1,500 m.; Alta Verapaz; Chiquimula. Costa Rica; Colombia; Venezuela.

Plants (at least ours) terrestrial; rhizome creeping, provided with rigid, lustrous, dark-brown scales, these lanceolate, 1-2 mm. long; leaves crowded to subfasciculate, 30-90 cm. long, long-petiolate; petiole 15-40 cm. long, about as long as the lamina, lustrous, yellowish brown to (most commonly) castaneous or blackish, nonalate, sulcate adaxially, quadrangular, but usually subterete at base; lamina thin- to firm-herbaceous, commonly 2-pinnate, with 2-6 pinnae and a conform, pinnalike terminal segment; rachis stramineous to dark brown, quadrangular, sulcate adaxially, nonalate; pinnae linear-lanceolate, rather strongly ascending, at 20-45° angles, sessile or short-stalked, somewhat reduced at base, strongly and gradually tapering to an often subcaudate apex; costae stramineous to reddish brown, deeply and narrowly sulcate adaxially; pinnules spreading to slightly ascending, sessile or subsessile, larger ones 0.9-1.3 cm. long, 0.4-0.6 cm. broad, 1.5-2 times longer than broad, those near pinna apex many times

shorter than the longer, central ones, the acroscopic margin incised, forming several shallow to deep lobes; veins commonly 1- to 2-forked, distinct; sori short, discrete, several along the acroscopic margin of segments; indusium 0.5 mm. broad, entire to somewhat erose.

Ours is the typical form. Kramer (1957) has described forma *lacera* from Colombia, which differs especially in its much more deeply and irregularly incised pinnules, with the sori placed at conspicuously different levels on the lobes.

Lindsaea lancea (L.) Bedd. Ferns Brit. India Suppl. 6. 1876. *Adiantum lancea* L. Sp. Pl. ed. 2. II: 1557. 1763. *L. trapeziformis* Dryander, Trans. Linn. Soc. 3: 43. 1797.

In forests and deeply wooded ravines, sea level to 400 m., Alta Verapaz; Izabal. West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Bolivia and Paraguay.

Plants terrestrial; rhizome creeping, provided with rigid, lustrous, orange to dark-brown scales, these linear to lanceolate, 1-2 mm. long; leaves approximate to crowded, or subfasciculate, 25-90 cm. long, petiolate; petiole 12-40 cm. long, about as long as the lamina, somewhat lustrous, stramineous to castaneous, darkest (often blackish) and terete at base, quadrangular above, with the angles often sharp and (abaxially) marginate or even faintly alate; lamina thin- or firm-herbaceous, pinnate or 2-pinnate, the 2-pinnate ones with 1-7 pairs of pinnae and a conform, pinnalike terminal segment; rachis stramineous to dark brown, sulcate adaxially, quadrangular, with the angles often sharp and marginate; pinnae (when present) lanceolate or oblong-lanceolate, spreading to somewhat ascending (at 45-60° angles), short-stalked or (distally) subsessile, not very strongly reduced at base, terminating rather abruptly in a relatively large, distinct, apical segment; costae stramineous to dark brown, flattened or broadly sulcate adaxially, quadrangular, the angles commonly sharp, often marginate, occasionally faintly alate; pinnules (or pinnae, on simply pinnate leaves) sessile to subsessile, to 2.8 cm. long and 1.2 cm. broad, commonly 2-2.5 times longer than broad, those near the pinna apex not strongly reduced (about ½ the length of the largest ones), the acroscopic margin entire; veins commonly 1- to 2-forked, distinct or indistinct; sori continuous along acroscopic margins and around the tip of the ultimate segment; indusium 0.2-0.3 mm. broad, the margin entire.

Kramer (1957) recognized five different varieties of *L. lancea*. Ours is the typical variety, and is widespread throughout the neotropics; the other four are essentially confined to South America.

Lindsaea portoricensis Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 326. 1811.

Apparently represented thus far in Guatemala by a single fragmentary specimen, Palmilla, Zacapa, Walker s.n. 1887 (ed. Donn.-Sm. 1203); also in British Honduras, on ridges and hummocks at or near sea level. Southern Mexico; Honduras; El Salvador; Greater Antilles; Trinidad; Colombia to the Guianas; Brazil; Peru; Bolivia.

Plants terrestrial; rhizome creeping, provided with rigid, lustrous, dark-brown scales, these mostly linear or linear-lanceolate, 1-2 mm. long; leaves approximate to crowded, 20-90 cm. long, petiolate; petiole 5-40 cm. long, much shorter than (in simply pinnate leaves) to about as long as the lamina, somewhat lustrous, yellowish brown to (more commonly) reddish brown or blackish, terete, or adaxially sometimes flattened and angular above (near the lamina); lamina firm-herbaceous to chartaceous, pinnate or 2-pinnate, the 2-pinnate ones with 1-3 pairs of pinnae and a conform, pinnalike terminal segment; rachis stramineous to dark brown, quadrangular, with the angles usually acute and sometimes marginate; pinnae (when present) lanceolate or oblong-lanceolate, very strongly ascending (often nearly vertical), sessile or very short-stalked, scarcely reduced at base, but reduced very gradually to a subattenuate apex; costae stramineous to dark brown, terete at base, otherwise quadrangular, the angles commonly acute and lighter colored, sometimes marginate (but not alate); pinnules (or pinnae, on simply pinnate leaves) sessile or subsessile, larger ones 0.5-1.5 cm. long, 0.3-0.7 cm. broad, commonly twice as long as broad, becoming gradually and conspicuously reduced toward pinna apex, the acroscopic margin subentire (to rarely crenulate); veins 1- to 3-forked, commonly distinct; sori continuous along the acroscopic margin and often around the tip of the ultimate segment; indusium 0.3-0.4 mm. broad, the margin erose.

There are few significant differences between this and *L. stricta*, and it might just as well be considered merely another variant of the latter.

***Lindsaea quadrangularis* Raddi, ssp. *subalata* Kramer, Acta Bot. Neerl. 6: 190. 1957.**

In forests, commonly along or near shores of lakes or banks of rivers, at or near sea level; Izabal. Cuba; southern Mexico to Colombia.

Plants terrestrial; rhizome creeping, provided with rigid, lustrous, dark-brown scales, these linear to lanceolate, 1-2 mm. long; leaves approximate to crowded, 25-80 cm. long, petiolate; petiole 15-40 cm. long, about as long as the lamina, somewhat lustrous, yellowish brown to (most commonly) dark reddish brown, quadrangular (above the subterete base) and often sulcate, the angles obtuse, nonalate; lamina thin- to firm-herbaceous, 2-pinnate, with (2) 3-7 pairs of pinnae and a conform, pinnalike terminal segment; rachis yellowish to reddish brown, terete to quadrangular, adaxially often broadly sulcate, with the angles acute and often pale-marginate, but not alate (at least below the terminal segment); pinnae sessile or subsessile, lanceolate, spreading to ascending (at 30-60° angles), rather strongly reduced at base, gradually and strongly reduced to the apex; costae yellowish to reddish brown, quadrangular, the angles commonly acute and (at least abaxially) alate, the wings 0.1-0.3 mm. broad; pinnules sessile or subsessile, larger ones 1.1-1.5 cm. long, 0.4-0.6 cm. broad, commonly 2-2.5 times as long as broad, becoming gradually and conspicuously reduced toward pinna apex, the acroscopic margin entire to crenulate; veins 1- to 2-forked, distinct (in ours) to indistinct; sori continuous along the acroscopic margin; indusium 0.2-0.3 mm. broad, the margin subentire.

***Lindsaea stricta* (Sw.) Dryander, Trans. Linn. Soc. London 3: 42. 1797.**

Plants terrestrial; rhizome creeping, provided with rigid, lustrous, dark-brown scales, these linear or lanceolate, 1-2 mm. long; leaves approximate to crowded, commonly 20-80 cm. long, short- to long-petiolate; petiole 2-30 cm. long, variable, much shorter to somewhat longer than the lamina, dull or somewhat lustrous, yellowish to blackish,

terete to subquadrangular, usually flattened or broadly sulcate adaxially, nonalate; lamina firm-herbaceous to subcoriaceous, pinnate to 2-pinnate (rarely 3-pinnate), the bipinnate ones with 1-7 pairs of pinnae and a conform, pinnalike terminal segment; rachis stramineous to dark brown, terete to quadrangular, nonalate; pinnae (when present) linear to linear-lanceolate, spreading to very strongly ascending, sessile or subsessile, slightly reduced at base, reduced strongly, but very gradually, to a minute, indefinite apical segment; costae stramineous to dark brown, terete at base, distally becoming obtusely to acutely quadrangular, nonalate; pinnules (or pinnae, on simply pinnate leaves) sessile or subsessile, larger ones 0.4-1 cm. long, 0.3-0.8 cm. broad, commonly 1-1.5 times as long as broad, the acroscopic margin subentire; veins 1- to 2-forked, indistinct to obscure; sori continuous along the acroscopic margin and often around the tip of the segment; indusium 0.3-0.5 mm. broad, the margin subentire to erose or lacerate.

This is a highly variable species with wide distribution in the neotropics. Only one collection has been reported from Guatemala to date, and this an intermediate between forma *stricta* and forma *moritziana*: *Weatherwax 225*, Quiriguá, Izabal. Since both forms occur in scattered locations in Mexico and Central America, they are to be expected in Guatemala and thus are described here.

Lindsaea stricta* forma *moritziana* (Kl.) Kramer, Acta Bot. Neerl. 6: 228. 1957. *L. moritziana* Kl. Linnaea 18: 548. 1844. *p.p.

Mexico; British Honduras; Costa Rica; Panama; Colombia; Venezuela.

Petiole commonly as long as or longer than the lamina; lamina 2-pinnate or (very rarely) 3-pinnate, firm-herbaceous to chartaceous; pinnae spreading to weakly ascending (at 40-80° angles); indusium subentire or slightly erose.

***Lindsaea stricta* forma *stricta*. *Adiantum strictum* Sw. Nov. Gen. Sp. Pl. Prodr. 135. 1788.**

Mexico; British Honduras; Nicaragua; Costa Rica; Panama; Colombia to the Guianas, south to Brazil and Bolivia; Trinidad; Cuba; Jamaica.

Petiole length variable, sometimes as long as the lamina, but most often (especially on simply pinnate leaves) very short; lamina 2-pinnate or (much more commonly) simply pinnate, subcoriaceous; pinnae strongly ascending (at 20-30° angles); indusium erose to lacerate.

LLAVEA Lagasca

Plants erect, terrestrial or epipetric; rhizome compact, erect, densely clothed with lanceolate, narrowly acute scales, these 1-1.5 cm. long, with margins entire, variously colored—stramineous, tan, brown, to lustrous black (scales of each color may be found on the same rhizome); leaves 20-100 cm. long, 8-35 cm. broad, partly dimorphous, distally fertile, proximally sterile, the fertile segments greatly contracted in width; petiole 10-50 cm. long, smooth, terete to subquadrangular, adaxially canaliculate, at base densely scaly as on the rhizome, the scales stramineous to tan; lamina 2-pinnate or (more



FIG. 43. *Llavea cordifolia*. a, habit, $\times \frac{1}{2}$; b, pinnule base, adaxial side, showing configuration of axes, $\times 6$; c, fertile segments, $\times 6$; d, rhizome scales, showing color gradation, $\times 6$.

commonly) 3-pinnate, glabrous, subcoriaceous, ovate to deltoid, fertile for $\frac{3}{4}$ of its length or only near the apex; pinnae strongly ascending, stalked, the costae adaxially furrowed, the raised ribs continuous onto the corresponding ribs of the rachis; ultimate segments obviously stalked, apical one conform, but usually somewhat larger than the lateral ones, lateral sterile ones to 6 cm. long and 1.8 cm. broad, lanceolate to ovate, acute or subacute at the apex, cuneate to truncate at the equilateral or inequilateral base, the margin serrulate and somewhat cartilaginous; veins free, 1- to several-forked, distinct, running fully out to the margin. Fertile segments linear, to 5.5 cm. long and 0.5 cm. broad, apiculate, truncate to cordate at base; sporangia stalked, borne along the veins, copious and confluent so as to cover the entire abaxial surface of the segment (thus appearing acrostichoid); indusia lacking, but sporangia partly protected by the sometimes reflexed, narrow segment margin; paraphyses lacking; spores commonly trilete and tetrahedral, but sometimes reported as bilateral, perine probably present, but thin and inconspicuous.

Llavea is a very distinct, monotypic genus, quite restricted in range. It occurs in eastern and southern Mexico and in northwestern Guatemala. In its partly dimorphic leaves and the shape of its segments it superficially resembles *Osmunda regalis*, but should hardly be confused with any other fern.

Llavea cordifolia Lag. Gen. et Sp. Pl. 16. 1816.

In moist soil of forests, thickets, and wooded ravines, but more commonly found on exposed rocky banks and crevices and ledges of cliffs, 1,200-3,500 m.; Alta Verapaz; Huehuetenango; El Quiché. Mexico. (Luis D. Gómez P. has personally reported to me that he has found the species in Pcia. Guanacaste, Costa Rica. If so, this represents an interesting disjunction in range.)

Characters are those of the genus.

LOMARIOPSIS Fée

REFERENCES: L. M. Underwood, The American species of *Stenochlaena*, Bull. Torrey Bot. Club 33: 591-605. 1907. R. E. Holttum, On *Stenochlaena*, *Lomariopsis* and *Teratophyllum* in the Malaya region, Gard. Bull. Straits Settlements ser. 3, 5: 245-316. 1932; and, The genus *Lomariopsis* in Madagascar and the Mascarene Islands, Notul. Syst. (Paris) 8 (1): 48-62. 1939; and, New species of *Lomariopsis*, Bull. Misc. Inform. 1939: 613-628. 1940.

Plants terrestrial (occasionally epipetric); rhizome woody, usually somewhat flattened, scandent, sparsely to densely scaly, the scales with margins often slightly to distinctly ciliate, not or obscurely clathrate; leaves dimorphous, commonly less than 1 m. long, approximate to remote, the axes variously scaly (the scales often minute and hairlike), the surface (especially abaxially) sometimes sparsely provided with minute squamulae; petiole not articulate, sparsely to amply (especially at base) scaly as on the rhizome, terete to subquadrangular, often shallowly canaliculate adaxially; lamina pin-

nate (or early leaves sometimes simple), terminating (at least in ours) in a pinnalike apical segment, glabrous or sparsely provided abaxially with minute squamulae; rachis terete to subquadrangular, canaliculate adaxially, sparsely scaly, the larger scales sometimes intermixed with filamentous squamulae; pinnae articulate at the rachis (but the pinnalike apical segment commonly continuous), sessile to rather short-stalked, the fertile ones similar in aspect to the sterile, but greatly contracted; veins free, numerous, commonly running to the somewhat cartilaginous margin; fertile pinnae with sporangia covering the abaxial surface (acrostichoid), lacking indusia and paraphyses; sporangia stalked, the stalks commonly with 3 rows of cells; spores monolete, bilateral, with (usually) folded perine.

The genus, as circumscribed here, contains about 40 pantropical species, subequally divided between the New and the Old World. Some of the species have been confused, due to the variability in the aspect of young or lower leaves (bathyphylls) as opposed to leaves (acrophylls) borne higher up on the climbing rhizome. The earlier leaves of some species may be simple, for example, whereas the acrophylls are fully pinnate. (See Holttum, 1939, p. 50; 1940, p. 614, for further discussion of this phenomenon.) Therefore careful observations must be made by collectors in the field, and proper label data supplied regarding the position of leaves collected. This may not be determined from a herbarium sheet.

- a. Pinnae 20-35 pairs, many of the proximal ones strongly reduced, those toward the base $\frac{1}{5}$ - $\frac{1}{2}$ as long as the larger, more distal ones; petiole of sterile leaf 2-7 cm. long. *L. vestita*.
- a. Pinnae 5-19 pairs, commonly only the basal ones (if any) reduced, these $\frac{1}{2}$ - $\frac{3}{4}$ as long as the larger ones; petiole of sterile leaf (9) 11-30 cm. long.
 - b. Largest sterile pinnae 4-6 cm. broad, with margin strongly cartilaginous; largest fertile pinnae 10-17 mm. broad; veins of sterile pinnae mostly 1 mm. apart. *L. japurensis*.
 - b. Largest sterile pinnae 1.4-2.4 cm. broad, with margin only slightly cartilaginous; largest fertile pinnae 1.5-8 mm. broad; veins of sterile pinnae mostly 1.5-2 mm. apart.
 - c. Scales of petiole base and rhizome dark yellow-brown to ferruginous, sparse, entire to minutely ciliate; largest fertile pinnae 4.5-8 mm. broad; altitude 1,000 m. or over. *L. latiuscula*.
 - c. Scales of petiole base and rhizome pale orange to whitish, ample to abundant, sparsely to amply ciliate; largest fertile pinnae 1.5-3.5 mm. broad; altitude 500 m. or below. *L. recurvata*.

***Lomariopsis japurensis* (Mart.) J. Sm. Hist. Fil. 140. 1875. *Acrostichum japurense* Mart. Icon Pl. Crypt. Bras. 86, t. 24. 1834.**

In wet forests, 20-600 m.; Alta Verapaz; Petén. British Honduras; Honduras; Nicaragua to Trinidad and the Guianas, south to Brazil and Bolivia.

Plants terrestrial, with high-climbing rhizomes; rhizome scales very dark brown, rigid, most of them appressed, lanceolate to linear-lanceolate, entire or (rarely) sparsely

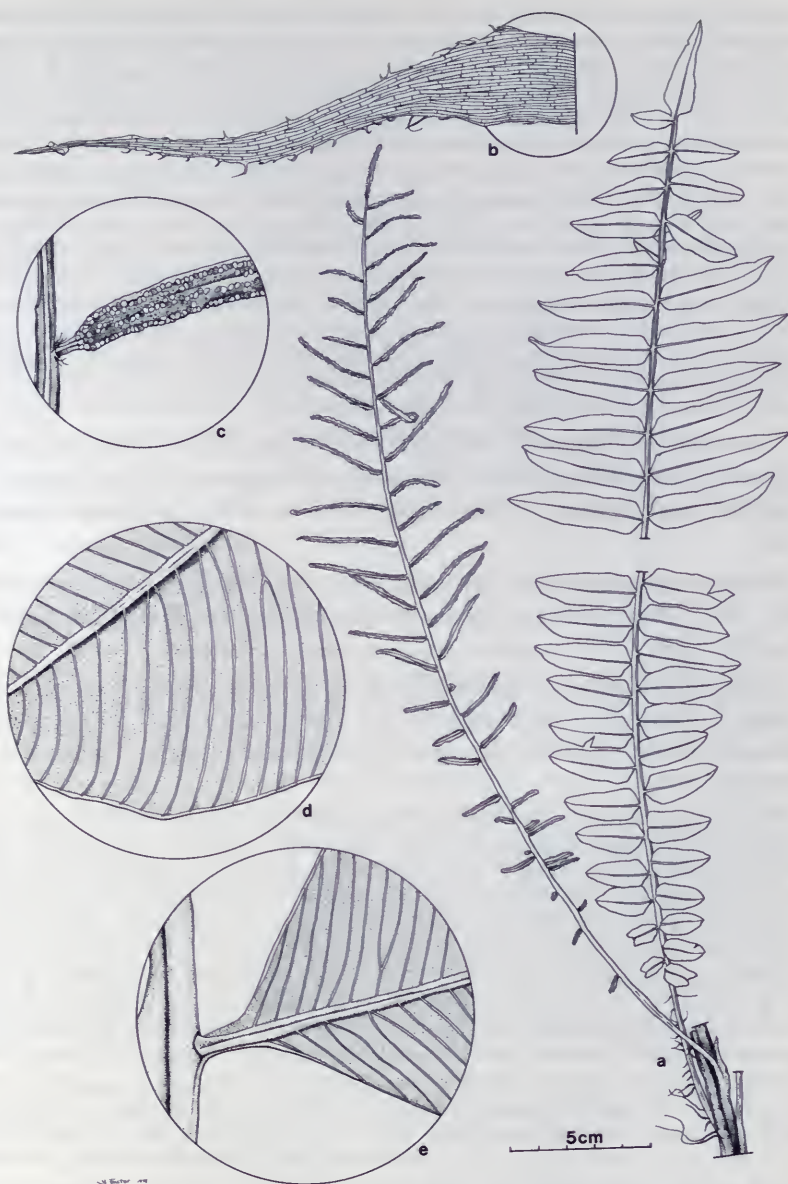


FIG. 44. *Lomariopsis*. a-b, *L. vestita*: a, habit, $\times \frac{1}{2}$; b, petiole scale, $\times 13$; c, *L. recurvata*, portion of rachis and pinna base, $\times 3\frac{1}{2}$; d-e, *L. japurensis*: d, portion of sterile pinna, showing venation, $\times 3\frac{1}{2}$; e, portion of rachis and pinna base, showing articulation, $\times 3\frac{1}{2}$.

setulose, 2-6 mm. long; leaves to 1 m. long. Sterile leaf to 30 cm. broad; petiole 18-30 cm. long, much shorter than the lamina, drying light to dark brown, scaly (especially at base) as on the rhizome, and also usually sparsely provided with minute, orange to light-brown, hairlike scales; lamina pinnate (or occasionally juvenile ones simple), chartaceous, ovate to broad-lanceolate, terminating in an apical segment nearly equal in size and shape to the largest pinna; rachis free, or narrow-marginate toward the apex, sparsely scaly (at least abaxially), the scales linear, dark brown to blackish, these sometimes intermixed with light-brown, filamentous squamulae; pinnae 5-13 pairs, most of them short-stalked, larger ones 15-20 cm. long, 4-6 cm. broad, basal ones somewhat reduced, lanceolate to elliptic-lanceolate, cuneate to broadly rounded at base, acuminate at the apex, the margin entire, the costa sparsely squamate and squamulate as on the rachis; veins simple or very rarely 1-forked, distinct, prominulous abaxially, numerous, about 1 mm. apart, spreading from the costa at a broad angle, extending fully to the veinlike, cartilaginous margin, sometimes abaxially provided with scattered orange to light-brown squamulae. Fertile leaf 12-26 cm. broad; petiole 10-30 cm. long; pinnae 8-15 pairs, short-stalked to (distally) subsessile, 8-17 cm. long, 1-1.7 cm. broad.

This is very similar to, and may even be conspecific with, the Brazilian *L. erythrodes* (Kunze) Fée [= *L. marginata* (Schrader) Kuhn]. See Morton (Contr. U.S. Natl. Herb. 38: 249. 1973) for further discussion.

Lomariopsis latiuscula (Maxon) Holttum, Bull. Misc. Inform. 1939: 617. 1940. *Stenochlaena latiuscula* Maxon, Contr. U.S. Natl. Herb. 10: 502. 1908.

Apparently known in Guatemala from a single, sterile specimen: in forest, Pansamalá, Alta Verapaz, alt. 1,200 m., Feb. 1887, *Tuerckheim* (ed. Donn.-Sm. 1129); (also possibly Quezaltenango?). Costa Rica; Panama.

Plants terrestrial, with a high-climbing rhizome; rhizome scales sparse, dark yellowish brown or ferruginous, lanceolate to linear, with margins entire or very sparsely and minutely ciliate; mature leaves to 70 cm. long. Sterile leaf 12-25 cm. broad; petiole 16-26 cm. long, yellowish to reddish brown, sparsely scaly as on the rhizome, and usually also provided with scattered, minute, ferruginous trichomes or filamentous scales; lamina pinnate, firm-herbaceous to chartaceous, lanceolate or deltoid-lanceolate, terminating in an apical segment similar in shape, but $\frac{1}{2}$ - $\frac{3}{4}$ the size of the larger pinnae, scarcely or not at all reduced at base; rachis marginate or narrow-alate distally, marginate or free proximally, sparsely to amply scaly, the scales linear to linear-lanceolate, deep orange to ferruginous, these commonly intermixed with ferruginous, filamentous squamulae or tortuous trichomes; pinnae 13-17 pairs, sessile to short-stalked, larger ones 9-13 cm. long, 1.6-2.2 cm. broad, lanceolate, narrowly to broadly cuneate at base, attenuate at apex, the margin crenulate-denticulate; veins simple or 1-forked, distinct, numerous, 1.5-2 mm. apart, terminating at or very near the slightly cartilaginous margin. Fertile leaf 12-14 cm. broad; petiole 9-18 cm. long; pinnae 9-13 pairs, stalked (1-3 mm.), larger ones 7.5-11 cm. long, 0.45-0.8 cm. broad.

The species is quite rare—represented in herbaria by only a handful of specimens from Costa Rica and Panama, and the one sterile specimen from Alta Verapaz (although a number of collections of *L. recur-*

vata are erroneously determined as *L. latiuscula*). It is possible this is but a variant of the Costa Rican *L. maxonii* (Underw.) Holttum, with which it shares a multitude of characteristics. Significantly, both are found at higher elevations (1,000-2,500 m.), whereas most other Central American species of *Lomariopsis* occur well below 1,000 m. *L. maxonii* apparently differs in its more abundant, pale-yellow or whitish petiole and rhizome scales, and the longer-stalked pinnae.

There are three specimens in the herbarium at Field Museum (Standley 86647, Steyermark 33817 & 33888) from Quezaltenango which may be *L. latiuscula*. These are small, juvenile plants, with strongly dentate pinnae, very reminiscent of the West Indian *L. sorbifolia*. (However, this is not an uncommon characteristic in juveniles of other species.) But these plants were collected at 1,200-1,500 m.; and all have the darker rhizome scales found on *L. latiuscula*.

Lomariopsis recurvata Fée, Mém. Fam. Foug. II (Hist. Acrost.): 68, t. 28. 1845. *Stenochlaena recurvata* (Fée) Underw. Bull. Torrey Bot. Club 33: 600. 1907.

In wet forests, 30-370 m.; Alta Verapaz; Izabal; Petén. Southern Mexico; British Honduras; Honduras.

Plants commonly terrestrial, with a high-climbing rhizome; rhizome scales very pale orange to whitish, lanceolate to linear, with margins sparsely or amply ciliate, 0.5-1 cm. long; mature leaves 40-80 cm. long. Sterile leaf 15-24 cm. broad; petiole (9) 11-24 cm. long, $\frac{1}{2}$ - $\frac{1}{2}$ as long as the lamina, drying gray- to yellow-brown, sparsely to abundantly scaly (especially at base), the scales similar to those of the rhizome; lamina pinnate, chartaceous, elliptic- or oblong-lanceolate, terminating in an apical segment similar in shape, but $\frac{1}{2}$ - $\frac{3}{4}$ the size of the largest pinna, scarcely or not at all reduced at base; rachis marginate or narrowly alate distally, marginate or free proximally, sparsely scaly (at least abaxially), the scales linear to linear-lanceolate, orange to whitish, these commonly intermixed with light-brown, filamentous squamulae or trichomes; pinnae 12-19 pairs, sessile, larger ones (8) 9-15 cm. long, 1.4-2.4 cm. broad, lanceolate, narrowly or broadly cuneate at base, acuminate or subattenuate at apex, the margin subentire to denticulate, the basal pair not or somewhat reduced; veins simple or 1-forked, distinct, abaxially prominent, numerous, 1.5-2 mm. apart, terminating just short of the slightly cartilaginous margin. Fertile leaf 8-22 cm. broad; petiole 7-20 cm. long; pinnae 14-17 pairs, sessile to short-stalked (2 mm.), larger ones 4.5-14 cm. long, 0.15-0.35 cm. broad.

Lomariopsis vestita Fourn. Bull. Soc. Bot. France 19: 250. 1872. *Stenochlaena vestita* (Fourn.) Underw. Bull. Torrey Bot. Cl. 33: 600. 1907. *L. guatemalensis* Presl in sched.

In wet forests and wooded ravines, sea level to 350 m.; Alta Verapaz; Izabal. Southern Mexico to Panama; probably also in the West Indies and Andean South America.

Plants terrestrial, with stout, woody, high-climbing rhizomes; rhizome scales light orange to (more commonly) very pale yellow or whitish, lanceolate to linear, with mar-

gins sparsely to amply ciliate, 1-1.5 cm. long; mature leaves 30-75 cm. long. Sterile leaf to 20 cm. broad; petiole 2-7 cm. long, drying yellow- to gray-brown, amply scaly (especially at base) as on the rhizome; lamina pinnate, firm-herbaceous to chartaceous, elliptic-lanceolate or (more commonly) oblanceolate, broadest well above the middle, strongly and gradually reduced toward the base, terminating in an apical segment similar in aspect to the distal pinnae; rachis conspicuously to narrowly alate, or at least marginate toward the base, sparsely scaly (at least abaxially), the scales linear to linear-lanceolate, orange to whitish, these often intermixed with light-brown, filamentous squamulae or tortuous trichomes; pinnae 20-35 pairs, sessile to short-stalked (stalks rarely to 1 mm. long), larger ones 4-10 (12) cm. long, 1-1.7 cm. broad, oblong-lanceolate, truncate or subcordate at base, acute to acuminate at apex, the margin subentire to denticulate, the basal pair $\frac{1}{2}$ - $\frac{1}{3}$ the length of the largest ones; veins 1-forked or (most of them) simple, distinct, slightly prominulous abaxially, numerous, about 1 mm. apart, extending fully to the slightly cartilaginous margin. Fertile leaf to 16 cm. broad; petiole 4-12 (14) cm. long; pinnae 20-35 pairs, sessile or short-stalked (to 1 mm. long), larger ones 3.5-7.5 (10) cm. long, 0.15-0.2 cm. broad.

This may be conspecific with *L. fendleri* D.C. Eaton of Andean South America. I have not seen the type of the latter, but from the descriptions and the specimens examined, *L. fendleri* seems to differ only in its somewhat broader (to 3 mm.) fertile pinnae.

LONCHITIS Linnaeus

REFERENCE: R. M. Tryon, The genera *Lonchitis* and *Blotiella*, in Taxonomic fern notes III, Contr. Gray Herb. 191: 93-100. 1962.

Plants terrestrial; rhizome short-creeping to ascending, thick, fleshy, lacking scales, but amply provided with tawny to medium-brown, septate trichomes, these commonly 1-2 mm. long; leaves often quite large, monomorphous, petiolate, pubescent to nearly glabrous, lacking scales; petiole not articulate, glabrous or pubescent, succulent and hollow near the base; lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatifid, thin- or firm-herbaceous, deltoid or ovate, tapering to a pinnatifid apex; pinnae ascending, subopposite to alternate, glabrous, or pubescent on axes and tissue; veins free (in ours) or basal veins of adjacent segments sometimes connected, thus forming costal or costular areoles; sori marginal, commonly elongated, borne nearer the sinus than the segment apex (on smaller lobes occasionally extending around the sinus); indusium submarginal, commonly elongated, flaplike, opening inward, membranaceous; paraphyses lacking; sporangia stalked, borne in a line along the commissure at the base of the indusium; spores trilete, globose-tetrahedral, with perine.

Lonchitis can be easily confused with the genera *Pteris* and *Blotiella* (the latter is not represented in Guatemala), for leaves of all three have much the same aspect, and all have similar marginal indusia. However, in *Pteris* the rhizome and (often) the petiole are scaly, whereas in *Lonchitis* these parts lack scales but are provided with septate trichomes. The spores of *Blotiella* (a predominantly paleotropical genus) are monolete and bilateral and venation is strongly areolate.



FIG. 45. *Lonchitis hirsuta*. a, lamina, $\times \frac{1}{2}$; b, costa and pinnule base, $\times 3$; c, portion of rachis with segmented trichomes, $\times 12\frac{1}{2}$.

Spores of *Lonchitis* are trilete and tetrahedral, and venation is free (or, in the Old World species, with some casual anastomosing).

The genus contains two species: *L. occidentalis* Baker, of tropical Africa, and the American *L. hirsuta*. They are quite similar, but the African species has an essentially glabrous lamina and some tendency toward areolate venation, *i.e.*, the basal veins of adjacent ultimate segments are sometimes connected by a transverse veinlet, thus forming some costal or costular areoles. Our species is usually strongly pubescent, with totally free veins.

Lonchitis hirsuta L. Sp. Pl. 1078. 1753. *Pteris laciniata* Willd. Sp. Pl. 5: 397. 1810. *P. hirsuta* (L.) J. Sm. J. Bot. (London) 4: 165. 1841. *Anisosorus hirsutus* (L.) Maxon, Sci. Surv. Porto Rico & Virgin Is. 6: 429. 1926.

In forests, thickets, or wooded ravines, sometimes on steep canyon walls, 400-1,500 m.; Alta Verapaz; Baja Verapaz; Escuintla; Guatemala; Izabal; Quezaltenango; Retalhuleu; Suchitepéquez. West Indies; southern Mexico; Honduras to Panama; Colombia; Venezuela; Surinam; Ecuador; Peru; Bolivia.

Leaves 1-2 m. long, to nearly 1 m. broad; petiole (on mature leaves) 30-90 cm. long, yellowish to deep brown, terete abaxially, several to many-ridged adaxially, sparsely to densely pubescent with septate trichomes; lamina commonly deltoid-ovate, the basal pinnae scarcely or not at all reduced, the tissue, axes, and veins sparsely to amply pubescent with septate trichomes; pinnae typically 12-16 pairs, short-stalked, commonly deeply 1-pinnatifid, but proximal ones occasionally to 2-pinnate-pinnatifid on larger leaves; ultimate segments entire to shallowly lobed; veins free, wide-spaced, typically 4-6 pairs on an ultimate segment and 1-forked, their tips not or scarcely enlarged, terminating at the marginal commissure bearing the sori, but ending short of the margin on sterile portions of segments; indusium somewhat to greatly elongated, subentire, thin, commonly scarious.

LOXOGRAMME (Blume) Presl

REFERENCE: E. B. Copeland, The genus *Loxogramme*, Philipp. J. Sci. Bot. 11: 43-47. 1916.

Plants small, epiphytic or sometimes epipetric; rhizome slender, creeping, commonly with densely tomentose roots, and scaly (at least around bases of petioles); leaves monomorphous (as in ours) or strongly dimorphous, crowded to widely spaced, sessile or very short-petiolate, not articulate at the rhizome; lamina simple, entire, linear, lanceolate or oblanceolate, commonly thick and fleshy, opaque, glabrous; veins immersed and obscure, copiously anastomosing, the areoles often with (at least a few) included free veinlets; sori elongated, sharply oblique to the costa, borne in a single row on each side of

the costa, superficial or somewhat impressed in the tissue abaxially; indusia lacking; paraphyses lacking (at least in ours); sporangia short-stalked; spores monolete or (rarely) trilete, planoconvex to biconvex or subglobose, lacking perine.

Loxogramme is a paleotropical genus of about 35 species, with a single representative in Mexico and Central America.

Loxogramme mexicana (Fée) C. Chr. Index Fil. Suppl. III: 125. 1934. *Selliguea mexicana* Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 177. 1850-52 (nom. nud.). *S. mexicana* Fée, Mém. Fam. Foug. 7: 43, t. 10, f. 4. 1857. *Grammitis salvinii* Hook. 2d Cent. Ferns t. 71. 1861. *Gym-*



FIG. 46. *Loxogramme mexicana*. a, habit, $\times \frac{1}{2}$; b, portion of lamina with some sporangia removed to show shallow depression in tissue, $\times 6\frac{1}{2}$; c, rhizome scale, $\times 13$.

nogramme salvinii (Hook.) Hook. Sp. Fil. 5: 157. 1864. *G. mexicana* (Fée) Bak. in Hook. & Bak. Syn. Fil. 387. 1868. *Polypodium mexicanum* (Fée) Salom. Nomencl. Gefäßskrypt. 308. 1883. *L. salvinii* (Hook.) Maxon, Contr. U.S. Natl. Herb. 13: 17. 1909.

In forests, on tree trunks, or sometimes on wet rocks, 900-2,100 m.; Alta Verapaz; Baja Verapaz; Escuintla; Guatemala; Jalapa; Quezaltenango; San Marcos. Southern Mexico; El Salvador; Nicaragua; Costa Rica; Panama.

Leaves monomorphic, sessile, erect or pendent, crowded to widely spaced along the rhizome; rhizome amply provided with castaneous or blackish scales, these 2-3 mm. long, lanceolate, obviously clathrate, commonly lustrous; lamina 6-22 cm. long, (0.5) 1-3.5 cm. broad, linear to (commonly) oblanceolate, acute at apex, tapering very gradually to a narrow base, the margin subentire, often becoming irregularly constricted and even revolute in dry conditions; costa prominulous and nearly percurrent adaxially, immersed and scarcely evident abaxially (or seen as a longitudinal band of lighter colored tissue); sori oval or oblong at maturity, impressed in the tissue, commonly lacking in the proximal $\frac{1}{3}$ or $\frac{1}{2}$ of the lamina.

This might be confused in Guatemala with *Antrophyum ensiforme* (particularly specimens of the latter with shorter and thicker sori). However, *L. mexicana* has slender, usually long-creeping rhizomes with most leaves borne at wide intervals, while rhizomes of *A. ensiforme* are short and thick and leaves are subfasciculate. Furthermore, the costa on *L. mexicana*, adaxially, is prominulous and nearly percurrent, whereas in *A. ensiforme* it is scarcely or not at all raised, and is usually evident only as a band of discolored tissue.

MAXONIA Christensen

REFERENCES: C. Christensen, *Maxonia*, a new genus of tropical American ferns, Smithson. Misc. Collect. 66 (9): 1-4. 1916; C. V. Morton, Another genus of ferns new to the United States, Am. Fern J. 51: 81-83. 1961.

Plants terrestrial, becoming scandent; rhizome 0.3-2 cm. thick (often to 4 cm. including scales), long-creeping just beneath the soil and sparsely provided with attenuate, orange, golden, or brown scales, then emerging from the soil and becoming scandent, tightly adhering to tree trunks and densely clothed with scales; leaves distant, to 1 m. long, terrestrial ones sterile, those of the scandent rhizomes dimorphic, being either wholly fertile or sterile (or rarely an otherwise sterile leaf bearing a few fertile pinnules); petiole 30-60 cm. long, light brown to stramineous, smooth, essentially glabrous, rounded abaxially, sulcate adaxially, not articulate at the rhizome; lamina ovate, 3- to 4-pinnate, scarcely reduced at base, tapered gradually to a pinnatifid apex, subcoriaceous, glabrous except for the axes, which are commonly short-hispid on the adaxial side (often densely so); pinnae numerous, stalked, crowded to imbricate, ascending, segments and venation anadromous; axes deeply sulcate adaxially, the ribs conspicuously

decurrent onto the axes of the next order; sterile tertiary segments sessile, decurrent, obliquely ascending, acute, subdimidiate, broadly and deeply serrate to deeply and acutely lobed, margins plane, cartilaginous, the veins free, pinnately arranged, with branches strongly ascending, again 1- to 2-branched; fertile tertiary segments greatly constricted, commonly obtuse, margins revolute, the vein branches mostly simple; sori abaxial on the segments, borne on tips of veinlets, crowded or confluent, commonly extending beyond the segment margins; indusium broad, persistent, peltate, subreniform with a broad sinus or circular with a very narrow sinus; paraphyses none; sporangia long-stalked; spores monolete, bilateral, with perine, brown, echinate.

Some interesting differences have been observed (T. G. Walker, Brit. Fern Gaz. 10: 241-250. 1972.) between portions of the plant rooted in the soil and those climbing trees. Rhizomes growing beneath the soil are more rounded, with a rather sparse covering of scales, and bear only sterile leaves. However, when a rhizome emerges from the soil and begins to climb, it is covered by a thick matting of scales and flattens somewhat to conform with the tree trunk, to which it tightly adheres by means of stout roots. In the climbing stage, the leaves become dimorphous, an occasional fertile lamina alternating with the sterile ones.

The genus contains a single species, confined to southern Florida, Cuba, Jamaica, and disjunct areas of Central and South America. In its obliquely dissected, dimorphous leaves it superficially resembles some decomposed species of *Polybotrya*. However, sporangia of the latter are spread across the abaxial surface of segments, lacking indusia, whereas those of *Maxonia* are grouped in conspicuous sori, with persistent, peltate indusia. In Guatemala, the genus is represented by a variant of the species.

Maxonia apiifolia (Sw.) C. Chr. var. *dualis* (Donn.-Sm.) C. Chr. Smithson. Misc. Collect. 66 (9): 4. 1916. *Nephrodium duale* Donn.-Sm. Bot. Gaz. 15: 29. 1890.

In wet forests, on slopes and ravines, climbing tree trunks, 500-1,200 m.; Alta Verapaz (type from Pansamalá, *Tuerckheim 1408*); Izabal. Honduras; Nicaragua; Panama; Ecuador.

Characters of the genus; according to Christensen, differing from the typical variety in that the margins of rhizome scales are entire rather than erose or dentate, and that the leaves are larger and the rhizomes thicker.

Of the characters Christensen used to delineate var. *dualis* from the typical, only that of the rhizome scales is reliable. In comparing a number of specimens throughout Cuba, Jamaica, and Central America, the size of lamina and thickness of rhizome are seen to vary considerably. However, in all the West Indian specimens, the margins of



FIG. 47. *Maxonia apiifolia* var. *dualis*. a, habit, $\times \frac{1}{2}$; b, apex of fertile pinna, $\times \frac{1}{2}$; c, juncture of rachis and costa, adaxial side, showing configuration of axes, $\times 2$; d, fertile segment, $\times 3$.

rhizome scales are rather obviously dentate to erose (especially at the tips). Scale margins on our plants are always entire, and as long as plants are collected with a portion of rhizome, there can be no difficulty in identification. In all the specimens examined the difference in scales has been consistent; thus, within the scope of this treatment, the plants in our area are provisionally maintained as var. *dualis*.

MILDELLA Trevisan

REFERENCE: C. C. Hall and D. B. Lellinger, A revision of the fern genus *Mildella*, Amer. Fern J. 57: 113-134. 1967.

Plants epipetric or terrestrial; rhizome branched, the branches creeping to ascending or erect, abundantly scaly, the scales concolorous or bicolorous, narrow and subentire; leaves essentially monomorphic, rather long-petiolate, of small to moderate size, to about 40 cm. long; petiole not articulate, light brown to blackish, rather lustrous, terete and essentially glabrous abaxially, adaxially flattened to sulcate and copiously beset with 1- to few-celled, short and (in ours) rigid, cylindrical to clavate trichomes; lamina pinnate-pinnatifid, tapering to a pinnatifid apex, essentially glabrous except for the abundant trichomes on the axes adaxially; pinnae several, the basal pair subopposite and inequilateral at base (more strongly produced basiscopically), the other pinnae becoming less dissected, less strongly inequilateral and gradually reduced distally; veins free, 1-(2-) forked or simple, reaching nearly to the segment margin, the tips enlarged to flaring; sporangia short-stalked, (commonly a pair) borne at each vein tip; indusium inframarginal, often inconspicuously so, much thinner (often scarious) than the segment margin, opening inwardly, continuous (at least in ours), with margin entire, erose or ciliate; paraphyses lacking; spores trilete, tetrahedral, with perine.

The genus is closely related to *Cheilanthes* (under which see further discussion), differing principally in the indusium, which is borne just within, and of completely different texture than the margin. In *Cheilanthes* the indusium is formed by the slightly to strongly modified, revolute or reflexed segment margin. Species of the latter vary from glabrous to variously pubescent or scaly. In *Mildella* the leaves are essentially glabrous, but adaxially the petiole and rachis are copiously provided with short, few-celled, usually stout and rigid trichomes—a rather peculiar type not found on *Cheilanthes*.

There are only eight species of *Mildella*: ours, which occurs in Mexico and Central America, another in Hispaniola, and the rest in Asia. These are plants of middle to upper elevations, found in moist or dry, usually rocky situations.

Mildella intramarginalis (Klf. ex Link) Trev. Rendic. Ist. Lombardo, Milano II. 9: 810. 1876.

Rhizome horizontal and creeping to ascending or erect, provided with linear-lanceolate, attenuate scales, these 3-4 mm. long, bicolorous, castaneous with lighter

brown margins; leaves crowded to densely caespitose, 12-35 cm. long, 3-14 cm. broad, long-petiolate; petiole 7-20 cm. long, equaling or much longer than the lamina, castaneous to atropurpureous, adaxially flattened or sulcate and densely beset with minute, stout, cylindric to subclavate, mostly 2-celled trichomes; lamina ovate, deltoid-ovate, or subpentagonal, pinnate-pinnatisect (or again pinnatisect as to basal pinnae), with 2-5 free pairs of pinnae and a deeply pinnatifid apical section, firm-herbaceous to chartaceous, glabrous, except densely puberulent adaxially along the rachis and bases of costae; pinnae sessile or subsessile (or the basal pair very short-stalked), ovate or deltoid, at least the basal pair conspicuously inequilateral, with the basal basiscopic segments strongly produced and often once again pinnatifid; ultimate segments linear and usually falcate or subfalcate, adnate to strongly decurrent basiscopically, the margins plane, entire to sharply and deeply serrate; veins obliquely ascending, distinct, the tips (at least on mature leaves) clavate to wide-flaring at the cartilaginous segment margin; indusium continuous from apex to base of segment, with margin entire to erose or ciliate.

Two varieties of *M. intramarginalis* are recognized, both of which occur in Guatemala.

- a. Margins of ultimate segments entire to crenulate or (rarely) broadly and shallowly serrulate; indusium entire or very slightly erose.
M. intramarginalis var. *intramarginalis*.
- a. Margins of ultimate segments serrate, commonly deeply and sharply so; indusium erose, long-ciliate. *M. intramarginalis* var. *serratifolia*.

Mildella intramarginalis var. **intramarginalis**. *Pteris intramarginalis* Kaulf. ex Schlect. & Cham. Linnaea 5: 613. 1830. *nom. nud.* *P. intramarginalis* Kaulf. ex Link. Hort. Reg. Bot. Berol. ed. 2, 2: 34. 1833 (as *P. inframarginalis*). *Cheilanthes intramarginalis* (Kaulf. ex Link) Hook. Sp. Fil. 2: 112. 1852. *Pellaea intramarginalis* (Kaulf. ex Link) J. Sm. Cat. Kew Ferns 4. 1856.

In forests and thickets, or occasionally in open areas, on rocks or rocky ground, or on clay banks, 1,300-2,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Zacapa. Mexico to Panama.

Margins of ultimate segments entire to crenulate or broadly serrulate; indusium entire, sometimes slightly crispate or undulate, rarely slightly erose.

Mildella intramarginalis var. **serratifolia** (Hook. & Bak.) Hall & Lell. Amer. Fern J. 57: 124. 1967.

In shaded or (occasionally) open areas, on rocks, or on rocky clay banks, 1,730-2,400 m.; Chimaltenango; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez; Sololá. Mexico.

Margins of ultimate segments commonly deeply and sharply serrate (especially on mature leaves); indusium erose, long-ciliate, often so broad that those on each side of the segment nearly meet over the midrib.

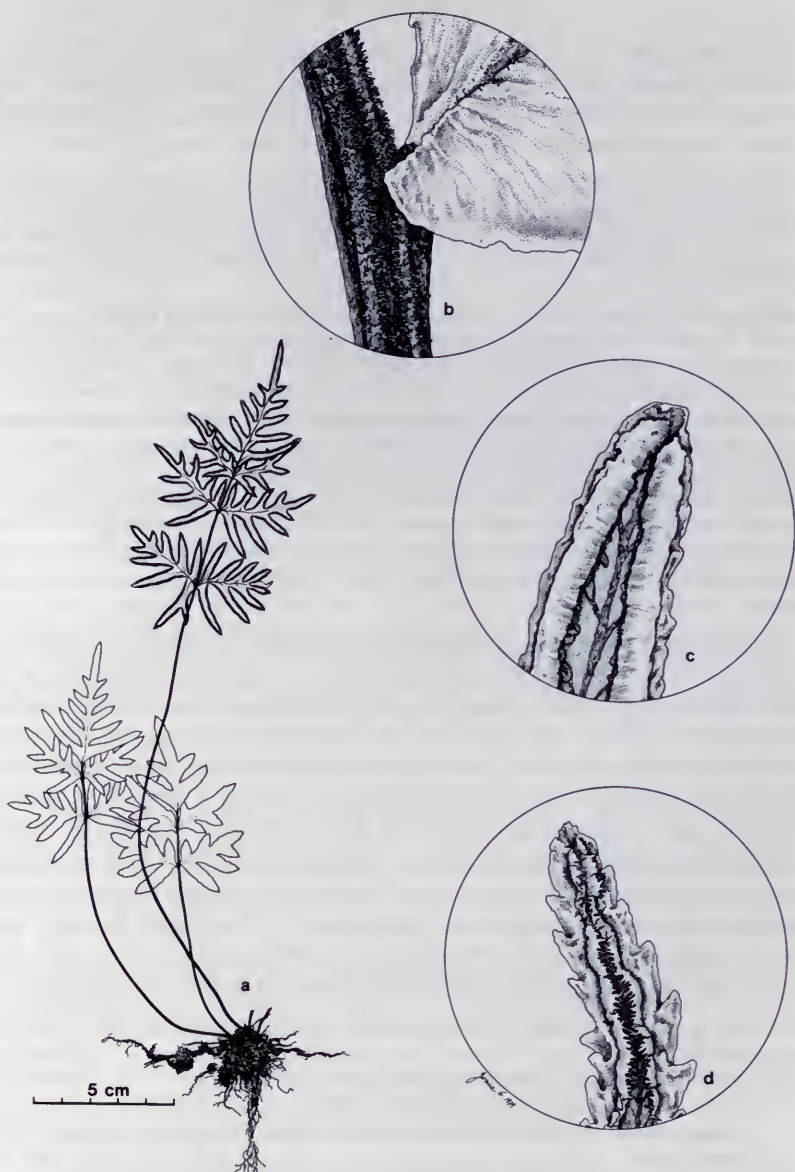


FIG. 48. *Mildella intramarginalis*. a-c, var. *intramarginalis*: a, habit, $\times \frac{1}{2}$; b, adaxial side of rachis, showing trichomes in groove and on ridges, $\times 12\frac{1}{2}$; c, tip of fertile pinna with subentire indusia, $\times 12\frac{1}{2}$; d, var. *serratifolia*, tip of fertile pinna with ciliate indusia, $\times 12\frac{1}{2}$.

NEPHROLEPIS Schott

REFERENCES: C. V. Morton, Observations on cultivated ferns, V. The species and forms of *Nephrolepis*, Amer. Fern J. 48: 18-27. 1958. Rolla M. Tryon, *Nephrolepis*, in: The ferns of Peru, Polypodiaceae, Contr. Gray Herb. 194: 225-234. 1964.

Plants with medium-sized to very long leaves, terrestrial, epiphytic, or epipetric; rhizome erect or ascending, scaly, often bearing numerous stout or wiry stolons; leaves essentially monomorphic, erect, arching, or pendent; petiole not articulate, sparsely to amply scaly, the scales sometimes reduced to, and intermixed with, pluricellular trichomes; lamina linear or linear-oblong, thin-herbaceous to subcoriaceous, simply pinnate (not including some more highly dissected cultivars), tapering gradually to a pinatifid or poorly defined apex; somewhat to strongly reduced at base; rachis scaly or pubescent-scaly; pinnae numerous, spreading to slightly ascending, sessile to shortly petiolulate, conspicuously articulate at the rachis, commonly subfalcate, often inequilateral at base and slightly to strongly auriculate acroscopically, margins commonly crenate to serrate, or crenate-serrate; veins free, forked, the vein tips terminating short of the pinna margin (commonly) in hydathodes, these frequently crenate; sori abaxial on the pinnae, terminal on the acroscopic vein branch, suprasedial to submarginal (or continuous and marginal in at least 1 Asian species); indusium lunate, reniform, hippocrepiform or circular, the sinus acute and narrow to broad and shallow, or sometimes lacking; paraphyses lacking; sporangium stalked; spores monolete, bilateral, occasionally with perine.

Nephrolepis is a pantropical genus of about 30 species. It is characterized by simply pinnate, long and narrow lamina, free veins, scaly and often stoloniferous rhizomes, and the suprasedial to submarginal sori with circular to reniform indusia. A few of the species are noted for their greatly elongated laminae, which may hang pendent from tree trunks or the edge of cliffs, sometimes attaining a length of several meters, yet no more than 20-25 cm. broad. Several species are quite easy to grow, either in tropical or subtropical gardens, or as houseplants in temperate regions. One of the most popular of all ferns for use in cultivation is *N. exaltata* cv. *bostoniensis*. This, with its many cultivars, has been a favorite of gardeners and homeowners for well over a century. The following species are known to occur in Guatemala.

- a. Indusium lunate to reniform (sinus broad and shallow, or lacking), mostly opening toward pinna apex.
- b. Pinnae (most of them) cuneate at base basiscopically. *N. pectinata*.
- b. Pinnae mostly rounded to cordate basiscopically.
 - c. Veins distinct; pinnae broadly or narrowly triangular, margin crenate to shallowly lobed. *N. occidentalis*.
 - c. Veins indistinct to obscure; pinnae oblong or lance-oblong, margin subentire to broadly and shallowly crenate. *N. cordifolia*.
- a. Indusium circular to hippocrepiform (sinus narrow to U-shaped), mostly opening toward pinna margin.
- d. Pinnae very strongly inequilateral at base, most of them basiscopically cuneate;

- pinnae abaxially glabrous to very minutely squamulose, the squamules usually stellate. *N. rivularis*.
- d. Pinnae subequilateral to somewhat inequilateral at base, basiscopically broadly rounded, truncate or auriculate; pinnae abaxially hirtellous or filiform-scaly.
- e. Pinnae not or scarcely auriculate at base acroscopically; tissue densely hirtellous (rarely glabrate) abaxially; petiole scales spreading, pale, filiform. *N. biserrata*.
- e. Pinnae (most of them) with a long, narrow, usually acute auricle at base acroscopically; tissue sparsely to amply filiform-scaly abaxially; petiole scales mostly appressed, often castaneous, with ciliolate or fimbriate margins. *N. multiflora*.

***Nephrolepis biserrata* (Sw.) Schott, Gen. Fil. t. 3. 1834. *Aspidium biserratum* Sw. J. Bot. (Schrader) 1800 (2): 32. 1801.**

In forests and thickets, or in clearings or on open banks, erect on the ground or on fallen logs, or pendent from tree trunks or steep banks, sea level to 400 m.; Alta Verapaz; Izabal; Petén; Zacapa. Florida; West Indies; Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil; Old World tropics.

Plants terrestrial or epiphytic; rhizome erect, often stout, provided with lustrous, orange to castaneous, lanceolate or linear-lanceolate, attenuate scales, these 3-5 mm. long, often lighter colored at the ciliolate or fimbriate margin, stolons numerous; leaves erect to pendent, to 3 m. long, mature ones (12) 14-24 cm. broad, crowded to subfasciculate, petiolate; petiole stout, mature ones 2.5-5.5 mm. thick, 12-60 cm. long, shorter than the lamina, dull or slightly lustrous, yellow- or gray-brown, abaxially terete, adaxially sulcate, sparsely provided with orange or light-brown, filamentous scales, these sometimes reduced to, and intermixed with, scattered, spreading pluricellular trichomes; lamina linear-oblong, firm-herbaceous to chartaceous; rachis yellow- or gray-brown, sulcate adaxially, amply provided with orange, filamentous, spreading scales, these reduced to, and intermixed with, long, spreading, pluricellular trichomes; pinnae short-stalked to subsessile, larger ones 8-14 cm. long, 1.2-2.4 cm. broad, subequilateral at base, rounded to truncate or (occasionally) subauriculate acroscopically, the margins crenate or obtusely serrate, or alternately crenate and serrate, the tissue adaxially glabrous, but the costa often sparsely to amply provided with pale, spreading, pluricellular trichomes 0.3-0.5 mm. long, the tissue and costa abaxially densely hirtellous (rarely glabrate) and the costa commonly with a few filiform scales; veins commonly 2-forked, distinct to obscure, the branch tips terminating short of the margin in slightly enlarged hydathodes, these usually dark (very rarely somewhat cretaceous); sori supramedial, not crowding the margin, usually distant from the margin by 1-4 times their diameter; indusia circular, most of them opening toward the pinna margin (but in mature ones sporangia spreading in all directions), the sinus narrow, often apparently lacking due to the touching or overlapping of the basal edges.

This is closely related to, and easily confused with, *N. multiflora*, under which see further discussion.

***Nephrolepis cordifolia* (L.) Presl, Tent. Pterid. 79. 1836. *Polypodium cordifolium* L. Sp. Pl. 1089. 1753. *Aspidium tuberosum* Bory**

ex Willd. Sp. Pl. 5: 234. 1810. *A. pendulum* Raddi, Opusc. Sci. 3: 289. 1819. *N. pendula* (Raddi) J. Sm. J. Bot. (London) 4: 197. 1841. *Cola de Quetzal*.

Rather common, in forests or in clearings, on fallen logs or on the forest floor, pendent from rocky cliffs or from trunks or branches of trees, sea level to 1,500 m.; Alta Verapaz; Escuintla; Guatemala; Izabal; Petén; Retalhuleu; Sololá; Zacapa; widely cultivated in other areas. Florida; Greater Antilles; Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia; Old World tropics.

Plants terrestrial, epipetric, or, more commonly, epiphytic; rhizome suberect, provided with orange to castaneous, linear to lanceolate scales, these 1-5 mm. long, stolons often bearing small, scaly tubers; leaves crowded, erect to arching or (more commonly) pendent, 0.4-3 m. long, 4-10 cm. broad, petiolate; petiole stout (1.5) 1.8-3 mm. thick, 8-30 cm. long, much shorter than the lamina, somewhat lustrous, light or dark brown, terete, or somewhat flattened adaxially, amply (at base) to sparsely scaly, the scales 1-3 mm. long, orange to castaneous, linear or lanceolate, with a broader, usually peltate base, deciduous, often leaving a small dark-brown or blackish dot; lamina linear, firm-herbaceous to subcoriaceous; rachis dark brown to yellowish, terete abaxially, flattened or shallow-sulcate adaxially, subglabrous, or often with a tuft of filiform scales at the base of each pinna (the scales commonly reduced to tortuous, simple trichomes); pinnae glabrous, sessile, or with very abbreviated stalks, larger ones 2-5 cm. long, 0.7-1.2 cm. broad, acute to broadly rounded, oblong, oblong-lanceolate, or subfalcate (usually with margins parallel or subparallel for most of their length), slightly to somewhat inequilateral at base, broadly rounded to subcordate basiscopically, more strongly produced and obtusely to acutely auriculate acropically, the auricle sometimes overlapping the rachis, margin subentire to broadly and shallowly crenate; veins 1-forked, indistinct to obscure, the branch tips terminating short of the margin in (often crenate) hydathodes; sori supramedial; indusium lunate or reniform, the sinus broad and shallow, or lacking, opening mostly toward the pinna apex.

This scarcely differs from *N. occidentalis*, under which see further discussion.

Nephrolepis cordifolia varies greatly in some of its characters, especially in length and texture of lamina. Typically, leaves are chartaceous to subcoriaceous, with tissue so opaque that veins are scarcely discernible or fully obscured. But some more delicate plants have been observed, with increasingly thinner texture, and in these the veins are (if not sharply outlined) at least evident. Even more striking is the variable length of leaves, which is probably determined by type of individual habitat. Typical *N. cordifolia*, common in the Old World and usually found in the neotropics on the ground or on fallen logs, is a stout, erect plant, with leaves less than 1 m. long. However, plants found on wet, rocky banks, or on trunks or low branches of trees are often arching to pendulous, and some hang to a length of 2-3 (or more?) m. These latter have been referred by some to a separate species, *N.*

pendula. Tryon (1964) states that he is unable to find another character by which such a distinction can be reinforced, and I fully agree with him.

Nephrolepis cordifolia is a fern popularly used for cultivation, and may be found in gardens and city parks all over Central America. This is the stout, erect form described above. Less commonly cultivated in Guatemala and elsewhere is the curious variant, *N. cordifolia* cv. *duffii*. This looks not unlike a *Jamesonia*, for its pinnae are very crowded, circular in outline, and usually 0.5-1 cm. long. The rachis also may be distally 1- or 2-forked. Morton wrote (1958) that in some areas this may escape from cultivation, but I have not found this reported in Guatemala.

Nephrolepis multiflora (Roxb.) Jarrett ex Morton, Contr. U.S. Natl. Herb. 38: 309. 1974. *Davallia multiflora* Roxb. Calcutta J. Nat. Hist. 4: 515, t. 31 (left hand). 1844.

In secondary forests and thickets, or in clearings or on open banks, 50-600 m.; Izabal; Petén. West Indies; Honduras; El Salvador; Costa Rica; Brazil; tropical Asia.

Plants terrestrial; rhizome ascending to erect, provided with lustrous, bright-brown to blackish, lanceolate or ovate scales, these 1-2 mm. long, with narrow, light-brown, ciliate or fimbriate margins, stolons numerous, stout to wiry; leaves erect, 0.3-1.8 m. long, 9-20 cm. broad, crowded to subfasciculate, short- to long-petiolate; petiole stout, mature ones 2-4.5 mm. thick, 10-25 cm. long, much shorter than the lamina, slightly lustrous, yellow- or gray-brown, abaxially terete, adaxially sulcate, amply provided with appressed scales much like those of the rhizome, these lustrous and castaneous (or if lighter brown, then with a dark basal spot); lamina linear or linear-lanceolate, chartaceous; rachis yellow- or gray-brown, sulcate adaxially, amply to densely provided with tawny, orange, or light-brown scales (often with a castaneous median stripe), these 2-4 mm. long, tortuous, and filiform; pinnae sessile or very short-stalked, larger ones 5-12 cm. long, 0.6-1.4 cm. broad, subequilateral or somewhat inequilateral at base, broadly rounded, truncate or auriculate basiscopically, similar acroscopically but the auricle commonly long, narrow, and acute, the margins crenate to serrate (often deeply and doubly so), the tissue adaxially glabrous, but the costa amply provided with minute (0.1-0.2 mm.), rather stout and rigid, pale-brown, pluricellular trichomes, the tissue and costa abaxially densely provided with long, mostly appressed, tawny to light-brown, long-attenuate scales; veins commonly 2-forked, indistinct to obscure, the branch tips terminating very near the margin in small, often cretaceous hydathodes; sori submarginal, indusia circular, most of them opening toward the pinna margin (but in mature ones sporangia spreading in all directions), the sinus narrow, often apparently lacking due to the touching or overlapping of the basal edges.

This is often found in herbaria determined as *N. biserrata* or *N. exaltata* (L.) Schott. From the former, *N. multiflora* differs by the characters listed in the key. For comparison with the latter, see discussion below, under "Excluded Species."

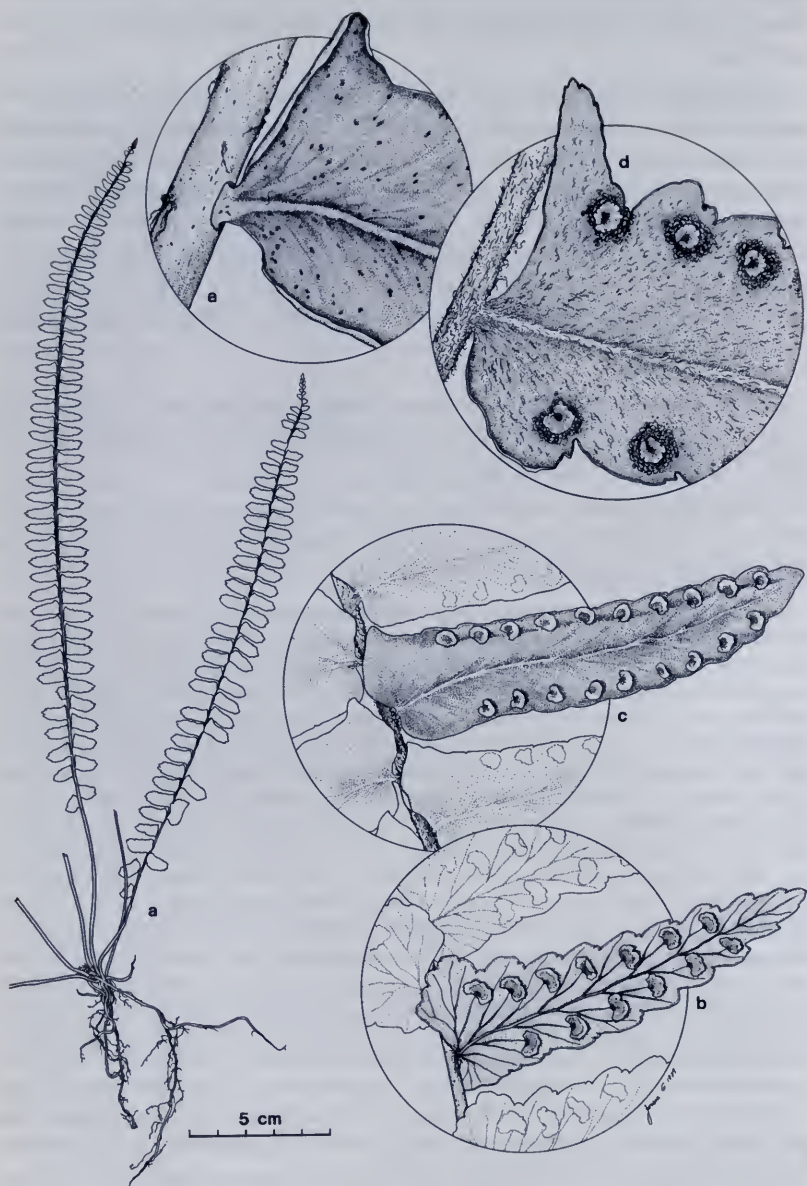


FIG. 49. *Nephrolepis*. a, *N. pectinata*, habit, $\times \frac{1}{2}$; b, *N. occidentalis*, fertile pinna, $\times 3$; c, *N. cordifolia*, fertile pinna, $\times 3$; d, *N. multiflora*, base of fertile pinna, $\times 6$; e, *N. rivularis*, portion of rachis and pinna base with scales removed to show articulation.

Nephrolepis multiflora is very closely related to (if not conspecific with) *N. hirsutula* (Forst.) Presl, a fern of tropical Asia. The latter is presumed to differ in the lack of short trichomes on costae adaxially (and in little else). A careful, worldwide study of the entire complex is needed to properly delimit such species as *N. biserrata*, *N. exaltata*, *N. hirsutula*, and *N. multiflora*.

***Nephrolepis occidentalis* Kunze, Linnaea 18: 343. 1844.**

Rare, in forests or wooded ravines, most often on rocks or rocky banks, occasionally on large mossy rocks in streams, 1,200-1,900 m.; Huehuetenango; Santa Rosa. Mexico; Honduras; El Salvador; Costa Rica; Panama; Colombia; Venezuela; Brazil; Peru.

Plants commonly epipetric, occasionally terrestrial; rhizome small, poorly developed, provided with orange, linear to filiform scales, these 1-2 mm. long, stolons often bearing small, scaly tubers; leaves few, crowded, erect to arching or pendent, 22-80 cm. long, 3-7 (8) cm. broad, short-petiolate; petiole wiry, 0.8-1.8 (2) mm. thick, 3-18 cm. long, much shorter than the lamina, somewhat lustrous, stramineous to yellow-brown, darker at base, terete proximally, flattened or angular distally, sulcate adaxially, amply (at base) to sparsely scaly, the scales 1-3 mm. long, orange, filiform, with a broadened, peltate base, often dark-spotted at point of attachment, these persistent as minute, blackish dots when the scales have fallen away; lamina lanceolate or linear-lanceolate, thin-herbaceous to membranaceous; rachis stramineous, subquadrangular, sulcate adaxially, subglabrous, but with a cluster of orange, filiform scales at the base of each pinna; pinnae glabrous, sessile, larger ones 2-3.5 (4) cm. long, 0.4-0.9 (1.2) cm. broad, acute or subacute, elongate-triangular and straight to (rarely) subfalcate, strongly tapering from broad base to apex, somewhat inequilateral at base, rounded to subauriculate basiscopically, more strongly produced and broadly auriculate acroscopically, the auricle round, strongly overlapping the rachis, margin crenate to shallowly lobed; veins 1- (2)-forked, quite distinct, the branch tips terminating short of the margin in (usually cretaceous) hydathodes; sori supramedial; indusium lunate or reniform, the sinus broad and shallow, or lacking, opening mostly toward the pinna apex.

This is closely related to, and may not merit specific distinction from, *N. cordifolia*. Although pinnae appear to differ *typically* in shape, margin, and texture, there seems to be enough variability in these to warrant further study, and perhaps a reappraisal of the relationship. The taxa do not differ significantly in any other features.

***Nephrolepis pectinata* (Willd.) Schott, Gen. Fil. 3. 1834. *Aspidium pectinatum* Willd. Sp. Pl. 5: 223. 1810.**

In forests, on rocks or rocky banks, on the forest floor, or on trunks or lower branches of trees, 800-1,600 m.; Alta Verapaz; Huehuetenango; Petén; San Marcos; Sololá. Mexico; Honduras to Panama; Colombia and Venezuela, south to Brazil and Bolivia; Greater Antilles.

Plants terrestrial, epiphytic, or (occasionally) epipetric; rhizome slender, suberect, sparsely to amply provided with light-brown to castaneous scales, these lanceolate or

linear-lanceolate, 1-3 mm. long; leaves erect to (rarely) pendent, 25-80 cm. long, 2.5-6 cm. broad, densely crowded, short- to long-petiolate; petiole wiry, 1-1.8 mm. thick, 3-30 cm. long, commonly much shorter than the lamina, somewhat lustrous, light brown, terete abaxially, sulcate adaxially, amply (at base) to sparsely scaly, the scales 1-2 mm. long, orange to castaneous, often ciliolate, with their bases broad and peltate and dark-spotted at point of attachment, these persistent as minute blackish dots when the scales have fallen away; lamina linear, firm-herbaceous; rachis light brown, sulcate adaxially, glabrous, but with a dense cluster of orange, tortuous, attenuate scales at the base of each pinna; pinnae glabrous, sessile or subsessile, 1.4-3 cm. long, 0.4-0.7 cm. broad, acute to obtuse, most of them strongly inequilateral at base, cuneate basiscopically, strongly produced and often sharply auriculate acroscopically, margin subentire or obtusely crenate-serrate; veins mostly 1-forked, indistinct or obscure, the branch tips terminating short of the margin in blackish hydathodes; sori supramedial; indusium lunate or reniform, the sinus broad and shallow, or lacking, opening mostly toward the pinna apex.

***Nephrolepis rivularis* (Vahl) C. Chr. Index Fil. 455. 1906. *Polypodium rivulare* Vahl, Eclog. Amer. 3: 51. 1807. *Nephrodium crenatum* Desv. Mém. Soc. Linn. Paris 6: 252. 1827.**

In forests, often on or near banks of streams, on the forest floor or pendent from tree trunks, 50-350 m.; Alta Verapaz; Izabal. West Indies; southern Mexico; Honduras to Panama; Colombia to the Guianas, south to Brazil and Peru.

Plants terrestrial or epiphytic; rhizome stout, erect, provided with light- to dark-brown, linear or lanceolate, attenuate scales, these 2-3 mm. long, commonly with lighter colored, ciliolate margins, the stolons stout and numerous; leaves stiffly erect to arching or pendent, 0.5-2 m. long, 5-11 cm. broad, crowded to subfasciculate, short- to long-petiolate; petiole stout, 2-4 mm. thick, 12-50 cm. long, commonly much shorter than the lamina, slightly lustrous, yellow- or gray-brown, terete abaxially, flattened to broadly sulcate adaxially, amply provided with lanceolate, long-attenuate scales, these 3-7 mm. long, appressed or (the longer ones) tortuous and spreading, castaneous to blackish or light brown (and then usually castaneous at base) the margin setulose or ciliolate; lamina linear, firm-herbaceous to chartaceous; rachis light or yellowish brown, sulcate adaxially, amply to densely provided with light- or dark-brown, hairlike scales; pinnae glabrous, but very sparsely and minutely squamulose abaxially, sessile or subsessile, larger ones 3-6 cm. long, 0.5-0.8 cm. broad, narrowly acute, very strongly inequilateral at base, cuneate to (less often) rounded basiscopically, much more strongly produced and acutely auriculate acroscopically, margin subentire to broadly crenulate or (toward the pinna apex) obtusely serrate; veins commonly 1-forked, indistinct, the branch tips terminating short of the margin in small, often cretaceous, hydathodes; sori supramedial to submarginal; indusium circular, commonly opening toward the pinna margin, the sinus narrow, often apparently lacking due to the touching or overlapping of the basal edges.

EXCLUDED SPECIES

***Nephrolepis exaltata* (L.) Schott, Gen. Fil. 3. 1834. *Polypodium exaltatum* L. Syst. Nat. ed. 10, 2: 1326. 1759.**

A number of Guatemalan specimens have been found in herbaria

identified as *N. exaltata*, but all those I have seen are actually *N. biserrata* or *N. multiflora*, incorrectly determined. Pinnae in *N. exaltata* are glabrous or sparsely and minutely squamulose, while the other two are either long, filiform-scaly or densely hirtellous on the abaxial surface. The base of the pinna in *N. exaltata* is broadly rounded basiscopically, and short- but acute-auriculate acroscopically. In *N. biserrata* the pinna base is nearly equilateral, rarely slightly (but never acutely) auriculate, and in *N. multiflora* it is very sharply, narrowly, and conspicuously auriculate acroscopically. Sori in *N. exaltata* are rather distant from the pinna margin, as in *N. biserrata*, but their shape is highly variable; *i.e.*, circular with a narrow, acute sinus in the proximal portion of the pinna, but becoming lunate or subreniform (with sinus broad or lacking), toward pinna apex. *Nephrolepis exaltata* is reportedly scattered around the world in tropical or subtropical regions, but it is to be assumed that many specimens in herbaria have been incorrectly so determined and that its true range is actually far more restricted.

Nephrolepis exaltata cv. *bostoniensis* does occur in Guatemala (and all over the world) as a most popular garden or potted plant. This is a cultivar with pinnae variously forked or dissected, and it may be found often in private gardens and public parks throughout Guatemala. It is possible that it may sometimes escape from cultivation (as reported elsewhere), but I have found no evidence of this to date.

NOTHOLAENA R. Brown

REFERENCES: R. M. Tryon, A revision of the American species of *Notholaena*, Contr. Gray Herb. 179: 1-106. 1956; I. W. Knobloch & D. S. Correll, *Notholaena*, in: Ferns and fern allies of Chihuahua, Mexico, Texas Research Foundation, Renner, Texas. 111-131. 1962.

Plants terrestrial or epipetric; commonly xerophytic; rhizome short-creeping to ascending or erect, scaly; leaves monomorphic, short- to long-petiolate, of small to moderate size; petiole not articulate, commonly castaneous to atropurpureous or blackish, lustrous, terete, scaly, pubescent, or glabrous, but usually with a few scales at base; lamina, in ours, pinnate-pinnatifid to nearly 3-pinnate, diminishing gradually or abruptly to a pinnatifid apex, farinose, pubescent, or scaly abaxially, pubescent to scaly or glabrous adaxially; rachis terete, or sometimes flattened to shallow-sulcate adaxially, pubescent to scaly, or glabrous; pinnae several to numerous, subequilateral, or in some species the basal pair inequilateral (much more strongly produced basiscopically at base); ultimate segments with fertile margins not or scarcely reflexed, not or only slightly modified (in *N. sulphurea* the margins strongly revolute but unmodified); veins free, the tips sometimes enlarged; sporangia stalked, borne at the tips or apical portion of veins; indusia essentially lacking; paraphyses lacking; spores trilete, tetrahedral, with perine.

Notholaena is very closely related to *Pellaea* and *Cheilanthes*, so closely so that some authors have included it with the latter. There is even conjecture that perhaps it would be best to unite all three genera. Lines of delimitation are indeed tenuous, thus the circumscription of the genus as attempted here is certainly open to challenge. To a large degree I have followed the revision of Tryon (1956). For further elaboration of the problems, see discussion of the genus *Cheilanthes*.

As recognized here, *Notholaena* contains about 50 species, most of them American. In Guatemala, the plants occur in various, frequently xeric, habitats, from 200 to 2,700 m. They may be found in shaded or exposed locations, and demonstrate a remarkable resistance to desiccation.

- a. Pinnae, at least abaxially, pubescent or scaly, not farinose (or if so the farina completely obscured by scales).
- b. Pinnae tissue obscured abaxially by dense matting of scales (also may be pubescent).
 - c. Rhizome scales atropurpureous to blackish; lamina 2-pinnate-pinnatifid; pinnae abaxially farinose (the farina obscured by the scales). *N. galeottii*.
 - c. Rhizome scales tawny to orange or ferruginous; lamina pinnate-pinnatifid; pinnae not farinose.
 - d. Rachis scales tawny to orange, subentire to denticulate; pinnae adaxially provided with tawny (occasionally whitish), arachnoid trichomes. *N. brachypus*.
 - d. Rachis scales mostly white, setulose to ciliate; pinnae adaxially glabrate or sparsely provided with white, pectinate scales which are often reduced to stellate trichomes. *N. sinuata*.
- b. Pinnae amply to densely pubescent, but lacking scales.
 - e. Lamina pinnate-pinnatifid, linear or narrow-elliptic, very strongly and gradually reduced at base; abaxial surface of pinnae completely obscured by dense tomentum. *N. aurea*.
 - e. Lamina 2-pinnate to nearly 3-pinnate, ovate or broadly lanceolate, slightly or not at all reduced at base; abaxial surface of pinnae sparsely to amply pubescent, but not completely obscured. *N. cinnamomea*.
- a. Pinnae glabrous, the abaxial surface conspicuously white- to yellow-farinose.
 - f. Lamina pinnate-pinnatifid, linear to narrow-elliptic, the basal pinnae somewhat or greatly reduced. *N. affinis*.
 - f. Lamina 2- (or more) pinnate, ovate, to deltoid, or pentagonal, the basal pinnae not or scarcely reduced.
 - g. Pinnae 2- to 3-pinnate, the secondary segments (pinnules) obviously stalked; rhizome scales brown, concolorous, not sclerotic. *N. incana*.
 - g. Pinnae (excluding the enlarged basal ones) pinnatifid or very rarely 2-pinnatifid, the secondary segments adnate; rhizome scales bicolorous, with a castaneous to blackish, sclerotic center and light-brown margins.
 - h. Petiole subequal to or slightly longer than the lamina; rhizome scales subentire, eglandular; farina white. *N. candida*.
 - h. Petiole commonly 2-4 times the length of the lamina; rhizome scales glandular-ciliolate (at least the more recent ones); farina white or yellow. *N. sulphurea*.

Notholaena affinis (Mett.) Moore, Index Fil. 233. 1861. *Cheilanthes affinis* Mett. Abh. Senckenberg Naturf. Ges. 3: 63. 1859.

On shaded, rocky slopes or ravines, most commonly in rocky crevices of cliffs, 200-1,200 m.; Chiquimula; El Progreso; Zacapa. Mexico; Honduras; El Salvador; Costa Rica.

Plants terrestrial or epipetric; rhizome short-creeping to ascending, provided with linear or lanceolate, lustrous, castaneous to blackish, sclerotic scales, these 2-3 mm. long, rigid, with setulose margins; leaves numerous, crowded to subcaespitose, 5-35 cm. long, 1-2.5 cm. broad, short-petiolate; petiole 1-6 cm. long, terete, lustrous, castaneous or atropurpureous to blackish, scaly at base, the scales like those of the petiole, or often a few with pale-brown, nonsclerotic centers; lamina pinnate-pinnatifid, chartaceous to subcoriaceous, linear or narrow-elliptic, tapering to both apex and base, the basal pinnae somewhat to strongly reduced; rachis terete, or slightly flattened adaxially, castaneous to atropurpureous or blackish, puberulent adaxially with short, stiff, brown, articulate trichomes, or (more often) glabrate; pinnae 10-24 pairs, spreading or weakly ascending, very short-stalked, articulate on the stalks, deltoid-ovate, pinnatifid (often deeply so), truncate and subequilateral at base, the abaxial surface densely yellow- (rarely whitish-) farinose, the adaxial essentially glabrous; veins 1- to 2-forked, obscure; sporangia borne at the vein tips, along the unmodified, scarcely (or not at all) reflexed segment margin.

Notholaena aurea (Poir.) Desv. Mém. Soc. Linn. Paris 6: 219. 1827. *Pteris aurea* Poir. in Lam. Encycl. Meth. 5: 710. 1804. *Acrostichum bonariense* Willd. Sp. Pl. 5: 114. 1810. *N. bonariensis* (Willd.) C. Chr. Index Fil. 6. 1905.

In forests or wooded ravines, on clay or rocky banks or hillsides, or more commonly on rocks or in rocky crevices of cliffs, 600-2,600 m.; Baja Verapaz; Chimaltenango; Huehuetenango; Jalapa; Jutiapa; Quezaltenango; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Sololá. Greater Antilles; southwestern United States; Mexico; Honduras; Nicaragua; Costa Rica; Colombia & Venezuela, south to Chile and Argentina.

Plants terrestrial or epipetric; rhizome short-creeping to suberect, provided with linear or linear-lanceolate, rigid scales, these 2-3 mm. long, bicolorous, lustrous-castaneous, with narrow, light-brown, subentire margins; leaves numerous, densely caespitose, 12-60 cm. long, 0.5-3.5 cm. broad, petiolate; petiole 3-15 cm. long, much shorter than the lamina, terete, lustrous, castaneous to atropurpureous or blackish, scaly only at base, amply provided with long, fine, delicate, pluricellular trichomes, these tawny to whitish, subappressed to weakly spreading; lamina chartaceous to subcoriaceous, linear or narrowly elliptic; tapering strongly both to apex and base, pinnate-pinnatifid; rachis terete, amply to copiously white- or tawny-pubescent as on the petiole; pinnae numerous, spreading to weakly ascending, sessile to short-stalked, oblong or deltoid-oblong, obtuse to subacute, pinnatifid (often deeply so), truncate and subequilateral at base, the abaxial surface completely obscured by a dense, whitish or tawny tomentum, adaxially rather sparsely to amply provided with whitish or yellowish, pluricellular, subappressed trichomes; veins 1- to 2-forked, obscure; sporangia borne at the vein tips, protected by a somewhat reflexed, narrow segment margin, which is often hyaline, or at least much thinner in texture than the rest of the segment.

Notholaena brachypus (Kunze) J. Sm. Ferns Brit. & For. 172. 1866. *Cheilanthes brachypus* Kunze, Linnaea 18: 341. 1844, and *op. cit.* 23: 307. 1850.

In forests or wooded ravines, on rocky banks or slopes, on rocks or rock outcrops or in crevices of cliffs, 200-2,000 m.; Escuintla; Huehuetenango; Jalapa; Jutiapa; Santa Rosa; Sololá; Zacapa. Mexico; Honduras; El Salvador; Nicaragua; Costa Rica.

Plants epipetric, or occasionally terrestrial; rhizome short, stout, erect, densely provided with orange to ferruginous scales, these 4-8 mm. long, linear, hair-tipped, their margins entire to sparsely denticulate; leaves numerous, caespitose, 4-25 cm. long, 1.8-4.5 cm. broad, nearly sessile to very short-petiolate; petiole 0.5-4 cm. long, somewhat lustrous, castaneous, terete, scaly as on the rhizome; lamina firm-herbaceous to chartaceous, pinnate-pinnatifid, narrow-elliptic to oblanceolate, abruptly reduced to a pinnatifid apex, gradually reduced toward base; rachis terete, generally obscured by a tomentum of tawny to orange, arachnoid trichomes, these partially covered by abundant, tawny to orange, lanceolate, attenuate, often denticulate scales; pinnae 8-18 pairs, spreading at broad (often 90°) angles from the rachis, subsessile, oblong-lanceolate, obtuse to subacute, truncate and subequilateral at base, lobed or pinnatifid, the lobes or segments 4-8 pairs, densely tomentose and scaly on the abaxial side as on the rachis, adaxially rather sparsely to amply provided with tawny or whitish, thin, arachnoid trichomes, neither surface farinose; veins simple or forked, obscure; sporangia borne at tips of veins, protected by the somewhat reflexed and often narrowly hyaline segment margin.

This and *N. sinuata* are superficially similar but, in addition to the key characters, they differ in a number of other respects. Leaves of the latter are generally rather obviously petiolate and most pinnae short-stalked, whereas leaves of *N. brachypus* are subsessile, to occasionally short-petiolate, and pinnae are subsessile. Pinnae margins in *N. sinuata* are unmodified and are scarcely or not at all reflexed. In *N. brachypus*, pinna margins are somewhat reflexed, and typically of thinner texture and lighter color (often hyaline) than the rest of the pinna.

Notholaena candida (M. & G.) Hook. Sp. Fil. V. 110. 1864. *Cheilanthes candida* M. & G. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 73. 1842. *N. sulphurea* (Cav.) J. Sm. var. *alba* Mett. ex Kuhn, Abh. Naturf. Ges. Halle 11: 32. 1869.

In forests or wooded ravines, on clay or rocky banks, on rocks or in crevices of rocky cliffs, 600-1,400 m.; Guatemala; Jalapa; Jutiapa; El Progreso; Santa Rosa. Mexico; Honduras; El Salvador; Nicaragua.

Plants terrestrial or epipetric; rhizome short-creeping, provided with lanceolate or ovate scales, these 2-4 mm. long, bicolorous, with a castaneous to blackish, sclerotic center, and light-brown, subentire (in ours) margins; leaves crowded to subcaespitose, 8-25 cm. long, petiolate; petiole 4-12 cm. long, commonly as long as or slightly longer than the lamina, terete, lustrous, atropurpureous to blackish, essentially glabrous, scaly

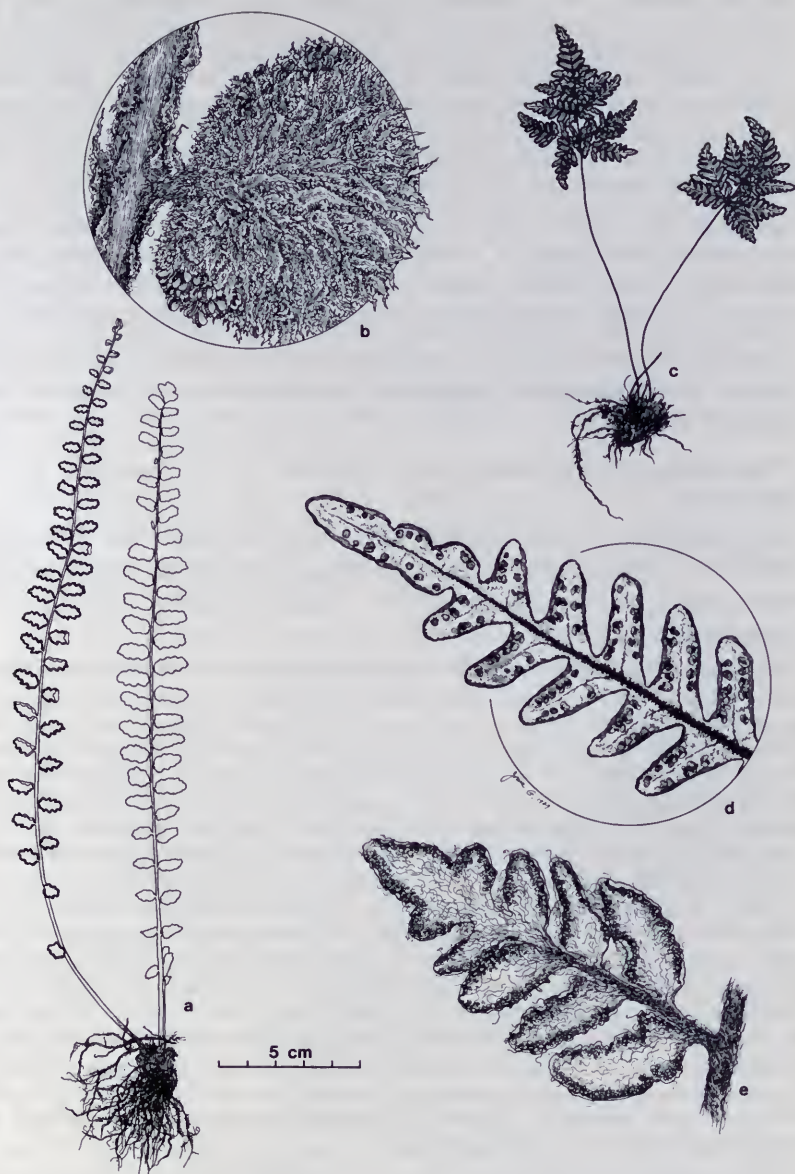


FIG. 50. *Notholaena*. a-b, *N. sinuata*: a, habit, $\times \frac{1}{2}$; b, portion of rachis and pinna base, abaxial side, $\times 12\frac{1}{2}$; c, *N. sulphurea*, habit, $\times \frac{1}{2}$; d, *N. candida*, pinna, abaxial surface, with farinose coating, $\times 6$; e, *N. cinnamomea*, pinna, $\times 6$.

only at base; lamina elongate- or ovate-pentagonal, 4-15 cm. long, 2.5-6 cm. broad, 2-pinnate-pinnatifid as to the enlarged basal pinnae, pinnate-pinnatifid to nearly 2-pinnate above, subcoriaceous, tapering (in ours) to a gradually pinnatifid apex, abaxially densely white-farinose, adaxially glabrous; rachis terete abaxially, flattened to sulcate adaxially, castaneous to atropurpureous, essentially glabrous; pinnae 6-12 pairs, sessile (or the basal ones short-stalked), the basal pair inequilateral, much more strongly produced basiscopically, secondary segments adnate; veins 1- to 2-forked, obscure; sporangia submarginal, borne on the vein tips, protected by the unmodified, discontinuously revolute segment margin, this usually rather erose or, at least, very irregular.

Ours is the typical variety of *N. candida*, the other being var. *copelandii* (Hall) Tryon of Texas and adjacent Mexican regions. The latter differs chiefly in its ciliate rhizome scales and in the leaf apex, which is abruptly contracted into a subconform terminal segment.

Notholaena candida and *N. sulphurea* are very closely related, and may be better considered varieties. See discussion of the latter for further comparison.

***Notholaena cinnamomea* Baker**, in Hook. & Bak. Syn. Fil. ed. 2: 515. 1874.

On shaded, clay banks or in moist earth among rock outcrops, 300-500 m.; Chiquimula; Escuintla; Zacapa (type from Motagua [as "Montagua"], *Salvin & Godman s.n.*, 1862). Apparently confined to Guatemala.

Plants terrestrial; rhizome short, erect, provided with linear or lanceolate, attenuate scales, these 2-3 mm. long, bicolorous, orange to light brown, with a broad, sclerotic, castaneous to blackish central portion and a lighter colored, narrow, entire margin; leaves numerous, crowded to caespitose, 7-20 cm. long, 2-4 cm. broad, petiolate; petiole 3-10 cm. long, as long as or shorter than the lamina, castaneous to atropurpureous or blackish, lustrous, terete, scaly (as on the rhizome) near the base, but distally the scales becoming tawny or orange, filiform, with a pectinate or pinnately branched base, and these grading into and intermixed with arachnoid, pluricellular trichomes; lamina thin-to firm-herbaceous, ovate or broadly lanceolate, 2-pinnate to nearly 3-pinnate, gradually reduced to a pinnatifid apex, slightly or not at all reduced at base; rachis terete, shallowly sulcate adaxially, rather abundantly provided with tawny to orange trichomes and scales as on the petiole; pinnae 6-12 pairs, weakly ascending, sessile or subsessile, oblong-lanceolate or narrow-triangular, obtuse, subtruncate and subequilateral at base; pinnules 4-8 pairs, subsessile, subentire to lobed or cut nearly or quite to the costule, somewhat inequilateral at base (often more strongly produced acroscopically), the lobes or segments obtuse, abaxially rather sparsely to amply pubescent with orange or tawny, arachnoid trichomes, adaxially glabrate or sparsely provided with whitish, filiform trichomes; veins 1- to 2-forked, obscure; sporangia borne at tips of veins, protected by an often reflexed, but scarcely modified margin.

***Notholaena galeottii* Fée**, Mém. Fam. Foug. V. (Gen. Fil.): 159. 1850-52 (type from Oaxaca, Mexico, *Galeotti 6565*). *N. arsenii* Christ, Notul. Syst. (Paris) 1: 232. 1910. *N. hyalina* Maxon, Amer. Fern J. 5: 4. 1915.

On rocks, on rocky slopes or in crevices of cliffs, in shaded or open areas, 1,500-2,000 m.; Huehuetenango. Mexico.

Plants epipetric or occasionally terrestrial; rhizome short-creeping to ascending, abundantly scaly, the scales 0.5-3 mm. long, triangular-lanceolate, rigid, often convexoconcave, lustrous, atropurpureous to blackish, conspicuously setose; leaves several, approximate to crowded, 6-35 cm. long, 2.5-6 cm. broad, petiolate; petiole 2-12 cm. long, much shorter than the lamina, lustrous, atropurpureous to blackish, terete, scaly at base as on the rhizome, but scales distally becoming shorter, thinner, and lustrous brown; lamina 2-pinnate or 2-pinnate-pinnatifid, subcoriaceous, elliptic-lanceolate, slightly reduced at base, tapering to a gradually pinnatifid apex; rachis terete, atropurpureous or blackish, densely covered with orange to castaneous, conspicuous setose scales; pinnae 15-30 pairs, spreading to slightly ascending, sessile or subsessile, elongate-triangular to oblong-lanceolate, obtuse, truncate and slightly inequilateral at base, with 7-10 pairs of lobed to pinnatifid pinnules, abaxially whitish farinose, but the farina completely obscured by a dense matting of scales, sparsely provided adaxially with simple, whitish trichomes, the costa shallowly sulcate adaxially; veins simple or forked, immersed, obscure; sporangia borne at the tips of veins, scarcely protected by the slightly (or not at all) reflexed, unmodified segment margin.

Notholaena incana Presl, Rel. Haenk. 1: 19, t. 1, f. 2. 1825. *Gymnogramma candida* Mett. Abh. Senckenberg Naturf. Ges. footnote 9. 1859 (not *N. candida* [M. & G.] Hook.). *Pellaea candida* (Mett.) Prantl, Bot. Jahrb. Syst. 3: 417. 1882.

On shaded or exposed rocks and stone walls and in crevices of cliffs, 1,500-2,700 m.; Huehuetenango; San Marcos; Sololá. Mexico; Hispaniola.

Plants commonly epipetric; rhizome short, erect or ascending, provided with linear-lanceolate to narrow-ovate, attenuate scales, these 4-10 mm. long, concolorous, not sclerotic, light brown to castaneous, dull to sublustrous, entire; leaves subcaespitose, 8-35 cm. long, 2-10 cm. broad, petiolate; petiole 3-18 cm. long, equaling or shorter than the lamina, terete, lustrous, atropurpureous to blackish, essentially glabrous, scaly only at base, lamina commonly 3-pinnate, chartaceous to subcoriaceous, deltoid to narrowly ovate, gradually tapering to apex, not or scarcely reduced at base; rachis terete, atropurpureous or blackish, essentially glabrous; pinnae 6-9 pairs, ascending, long-stalked, deltoid to ovate, subequilateral at base, with 3-6 pairs of stalked pinnules; ultimate segments articulate at their stalks, ovate, oblong, or nearly circular, densely white-farinose abaxially, glabrous adaxially; veins 1- to 2-forked, obscure; sporangia often covering all but the center of ultimate segments, the margin neither modified nor revolute.

Notholaena sinuata (Lag. ex Sw.) Kaulf. Enum. Fil. 135. 1824. *Acrostichum sinuatum* Lag. ex Sw. Syn. Fil. 14. 1806. *Cheilanthes sinuata* (Sw.) Domin, Biblioth. Bot. 20 (Heft 85): 133. 1913.

In and at edges of forests, in thickets, or in shaded ravines, on rocks or on rocky banks of ravines and rivers, 900-2,000 m.; Huehuetenango; El Quiché; San Marcos; Sololá. Hispaniola; southwestern United

States; Mexico; Honduras; Costa Rica; Colombia and Venezuela, south to Argentina.

Plants epipetric, occasionally terrestrial; rhizome short-creeping, rather stout, copiously provided with tawny, orange, or light-brown scales, these to 1 cm. long, linear, hair-tipped, their margins entire to setulose; leaves crowded to subcaespitose, 8-60 cm. long, 2-6 cm. broad, short-petiolate; petiole (3) 4-14 cm. long, light brown to castaneous, stout, terete, densely covered with whitish, linear or lanceolate, attenuate, setulose to ciliate scales; lamina subcoriaceous, pinnate to (in ours) pinnate-pinnatifid, linear to narrow-elliptic, gradually reduced both to apex and base; rachis terete, abundantly scaly as on the petiole; pinnae numerous, spreading to ascending, short-stalked, broadly oblong to ovate or triangular, obtuse to subacute, broadly rounded to truncate and sub-equilateral at base, subentire to (in ours) lobed or pinnatifid, the lobes or segments 3-6 pairs, abaxially obscured by tawny to orange, deltoid to lanceolate, fimbriate scales, these overlaying a thick tomentum composed of similar scales highly dissected into hairlike segments, adaxially glabrate or sparsely provided with whitish pectinate scales which are often reduced to stellate trichomes, neither surface farinose; veins 1- to 2-forked, obscure; sporangia borne at tips of veins, along the unmodified segment margin which is scarcely or not at all reflexed.

Ours is the typical variety of *N. sinuata*. Two other varieties were recognized by Tryon (1956), both occurring in the southwestern United States and Mexico. These differ from var. *sinuata* in their shorter, more obtuse pinnae, with fewer and smaller lobes and with adaxial scales coarser and more persistent. *Notholaena sinuata* might be confused with *N. brachypus*, under which see further comment.

Notholaena sulphurea (Cav.) J. Sm. Bot. Voy. Herald 1: 233. 1854. *Pteris sulphurea* Cav. Descr. Pl. 269. 1802. *N. cretacea* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 216 (seors. 64). 1849. *Cheilanthes cretacea* (Liebm.) Mett. Abh. Senckenberg Naturf. Ges. 5. 1859. *N. candida* (M. & G.) Hook. var. *lutea* Hook. Sp. Fil. 5: 111. 1864 (not *Pteris lutea* Cav. 1802).

Apparently represented in Guatemala from two collections: *O. F. Cook 270*, around Salamá, Baja Verapaz; *Bernoulli & Cario 307*, location unspecified. Mexico; Nicaragua to Colombia; Peru; Chile. Mostly in exposed areas, on rocky slopes, or in rock crevices of cliffs and canyon walls.

Plants usually epipetric; rhizome short-creeping, provided with linear-lanceolate to ovate scales, these 2-4 mm. long, bicolorous, with a castaneous to blackish, sclerotic center and light-brown, deciduously glandular-ciliolate margins; leaves crowded to subcaespitose, 6-20 cm. long, long-petiolate; petiole 4-16 cm. long, commonly 2-4 times as long as the lamina, terete, lustrous, atropurpureous to blackish, essentially glabrous, scaly only at base; lamina subpentagonal, 3-10 cm. long and often as broad, 2-pinnate-pinnatifid as to the enlarged basal pinnae, pinnate-pinnatifid above, subcoriaceous, tapering to a pinnatifid apex, abaxially densely white- or yellow-farinose, adaxially glabrous or sparsely farinose; rachis terete abaxially, flattened to sulcate adaxially, castaneous to atropurpureous, essentially glabrous; pinnae 4-8 pairs, subsessile, the

basal pair inequilateral, much more strongly produced basiscopically, secondary segments adnate; veins 1- to 2-forked, obscure; sporangia submarginal, borne on the vein tips, protected by the rather strongly (commonly continuously) revolute, but unmodified, segment margin, this subentire to erose.

This species, rare in Guatemala, is easily confused with *N. candida*. The characters used in the key are often inconstant and must be used in combination. The glands on the scales of *N. sulphurea* are often readily deciduous (and thus not observed), and of a number of leaves borne on a rhizome, several smaller (not necessarily immature) ones may have much shorter petioles. Laminae of *N. sulphurea* are commonly as broad as long, and whereas those of *N. candida* are typically 1.5-2.5 times as long as broad, a few may be seen nearly as broad as long. Although I maintain *N. sulphurea* as a distinct species for purposes of this treatment, it may be more accurate to follow Hooker (1864) in designating it a variety of *N. candida*.

In his revision (1956) Tryon cited Cook 270 (Baja Verapaz) as *N. candida*. Indeed the rhizome scales appear to lack glands, but very close scrutiny reveals some of the more protected ones to be quite glandular. Some leaves have long petioles, others do not, and the farina grades from white to a very pale yellowish hue. Thus it appears to be closer to *N. sulphurea* than to *N. candida*, and the collection serves as a good example of the intermediate condition which often exists between the two species.

Notholaena sulphurea also tends toward both *Pellaea* and *Cheilanthes*, because of its strongly revolute segment margins. See generic discussion of the latter for further elaboration.

ODONTOSORIA Fée

REFERENCE: W. R. Maxon, The genus *Odontosoria*, Contr. U.S. Natl. Herb. 17: 157-168. 1913.

Plants terrestrial, commonly scandent; rhizome relatively slender, creeping, abundantly scaly, the scales often narrow and rigid; leaves crowded to subcaespitose, large, often huge, monomorphous, of indeterminate growth, essentially glabrous; petiole relatively short, smooth (as in ours) or aculeate, not articulate; lamina commonly 3- or 4-pinnate, thin-herbaceous to chartaceous, glabrous, finely dissected; rachis straight to flexuous, smooth (as in ours) or aculeate, terete abaxially, flattened to broadly and shallowly sulcate adaxially; pinnae opposite or subopposite, widely spaced to crowded or imbricate, ascending to spreading (often at 90° angles), the costae straight or flexuous, smooth (as in ours) or aculeate; secondary and tertiary axes with raised, parallel ridges adaxially, the ridges continuous onto the axes of the next order above and below; ultimate segments quite small, cuneiform, obovate, or linear, entire to lobed or deeply cleft; veins free, simple or forked, terminating at the segment apex (or, in fertile segments, at the base of the sorus); sori terminal on the segments, borne at vein tips; paraphyses

lacking; indusium joined with the segment tissue at sides and base to form an involucre, open only at the distal end or, rarely, attached only at base and open at sides; sporangia slender-stalked, only a few to each sorus; spores trilete, globose-tetrahedral, with perine.

Odontosoria is a genus of about 10 species, confined to the neotropics. It is quite easily distinguished by its ample to huge, finely dissected leaves which are usually scandent and sprawling over other vegetation, its subopposite pinnae, and the cup-shaped involucre at the apices of segments. Some larger species of *Eriosorus* superficially may resemble *Odontosoria*, but indusia are lacking on the former, and sporangia are borne abaxially along the veins.

- a. Ultimate segments cuneiform, obdeltoid, or flabelliform, 1- or 2-cleft or -lobed; ultimate lobes 0.7-1 mm. broad (commonly broader than the indusium), narrowed at the fertile apex; indusium 0.3-0.6 mm. long, 0.2-0.4 mm. broad. . . . *O. guatemalensis*.
- a. Ultimate segments linear or narrow-clavate, simple or 1-forked; ultimate lobes 0.2-0.6 mm. broad (narrower than the indusium), commonly broadest at the fertile apex; indusium 0.7-1 mm. long, 0.5-0.8 mm. broad. *O. schlechtendalii*.

Odontosoria guatemalensis Christ, Bull. Soc. Bot. Génév. II. 1: 229. 1909 (type from Cuesta Grande, Hacienda de las Nubes, *Bernoulli & Cario 402.*)

In thickets, shaded ravines, or on open banks, often scandent or sprawling on surrounding vegetation, 650-1,700 m.; Chimaltenango; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; Suchitepéquez. Mexico (Chiapas).

Rhizome scales very slender, rigid, 3-6 mm. long, amber to castaneous, 3-6 cells (lumina) broad at base, long-tapering to a uniseriate, septate tip; leaves (mature ones) reaching 3-5 m. in length, erect, or larger ones leaning, sprawling, or scandent on surrounding vegetation; petiole 5-50 cm. long, stout, woody, terete (or slightly flattened adaxially), smooth and sublustrous, yellowish to reddish brown, lacking spines; lamina narrow-deltoid, 3- to 4-pinnate, thin- to firm-herbaceous; rachis straight to somewhat flexuous, yellowish to reddish brown, somewhat lustrous, lacking spines; pinnae stalked; costae slightly to strongly flexuous, smooth, bearing several to many stalked, alternate pinnules; ultimate segments cuneiform, obdeltoid, or flabelliform, cuneate at base, deeply cleft, or each of the divisions again deeply cleft, the ultimate lobes 0.7-1 mm. broad (broader than the indusium), commonly somewhat narrowed at the fertile apex; indusium 0.3-0.6 mm. long, 0.2-0.4 mm. broad, attached for most of its length to form an obturbinate, oblong, or elliptic involucre, bilabiate, the outer wall composed of scarcely or slightly modified leaf tissue, the inner wall thinner, yellowish to scarious.

Odontosoria schlechtendalii (Presl) C. Chr. Index Fil. 209. 1905. *Davallia divaricata* Schlecht. & Cham. Linnaea 5: 617. 1830. *nom. illeg.* (not Blume, 1828). *D. schlechtendalii* Presl. Tent. Pterid. 129. 1836. *Stenoloma schlechtendalii* (Presl) Fée, Mém. Fam. Foug. V. (Gen. Fil.) 330. 1852.



FIG. 51. *Odontosoria*. a, *O. guatemalensis*, central pinna, $\times \frac{1}{2}$; b-c, *O. schlechten-dalii*: b, central pinna, $\times \frac{1}{2}$; c, ultimate segments with sori, $\times 15$.

In forests, thickets, and shaded ravines, sometimes on open banks, 50-1,800 m.; Chiquimula; Huehuetenango; Izabal. Mexico; British Honduras; Honduras.

Rhizome scales very slender, rigid, 3-6 mm. long, amber to castaneous, 3-6 cells (lumina) broad at base, tapering to a uniseriate, septate tip; leaves (mature ones) to 3 m. long, erect to sprawling or scandent, or sometimes arching and pendent from steep banks; petiole 5-35 cm. long, stout, woody, terete (or slightly flattened adaxially), smooth and sublustrous, yellowish or grayish brown to (rarely) atropurpureous, lacking spines; lamina narrow-deltoid, commonly 4-pinnate, thin-herbaceous to chartaceous; rachis essentially straight, yellowish brown to castaneous or atropurpureous, somewhat lustrous, lacking spines; pinnae short-stalked; costae slightly to strongly flexuous, smooth, bearing several to many short-stalked to sessile alternate pinnules; ultimate segments simple and linear or narrow-clavate, or deeply 1-forked, the ultimate lobes 0.2-0.6 mm. broad, narrower than or equaling the indusium, commonly broadest at the apex, linear or narrow-clavate; indusium 0.7-1 mm. long, 0.5-0.8 mm. broad, attached for most of its length to form an obturbinate, oblong, or elliptic involucre, bilabiate, the outer wall composed of scarcely to slightly modified leaf tissue, the inner wall thinner, yellowish to scarious.

OLEANDRA Cavanilles

REFERENCES: W. R. Maxon, The American species of *Oleandra*, Contr. U.S. Natl. Herb. 17: 392-398. 1914. G. J. de Joncheere, The typification of *Oleandra articulata* (Filic.), Taxon 18: 538-541. 1969.

Plants terrestrial or epiphytic; rhizome long-creeping and often scandent (in ours) to erect or ascending, branching, scaly (usually densely so) and in some species conspicuously white-pruinose; leaves widely spaced to whorled, simple, entire, long-petiolate to sessile, attached to the rhizome by short or elongated bases (phyllopodia); petiole stout to wiry, glabrous, terete abaxially, sulcate adaxially, conspicuously articulate to the phyllopodium, the joint commonly swollen; lamina monomorphic (in Guatemala) to dimorphic, linear-lanceolate to oblong- or elliptic-lanceolate, the margins cartilaginous, entire or essentially so, firm-membranaceous to chartaceous, glabrous (in ours) to pubescent; costa conspicuous, distinct nearly to leaf apex, prominulous and commonly scaly (rarely pubescent) abaxially, sulcate adaxially; veins free, commonly 1-forked (especially near the base), crowded, running in parallel fashion out to the margin; sori round, borne abaxially on the veins, in 1 to several irregular rows between costa and margin, but generally much nearer the costa than the margin; indusium circular-reniform, attached proximally, at the sinus, persistent (at least in ours); paraphyses lacking; sporangia long-stalked (commonly with 3 rows of cells); spores monolete, bilateral, planoconvex, with perine.

Oleandra is a pantropical genus of about 40 species, not likely to be confused with any other. Its species are distinctive in their simple laminae with petioles clearly articulate above the rhizome, and in the reniform indusia borne on parallel free veins. The following occur in Guatemala.

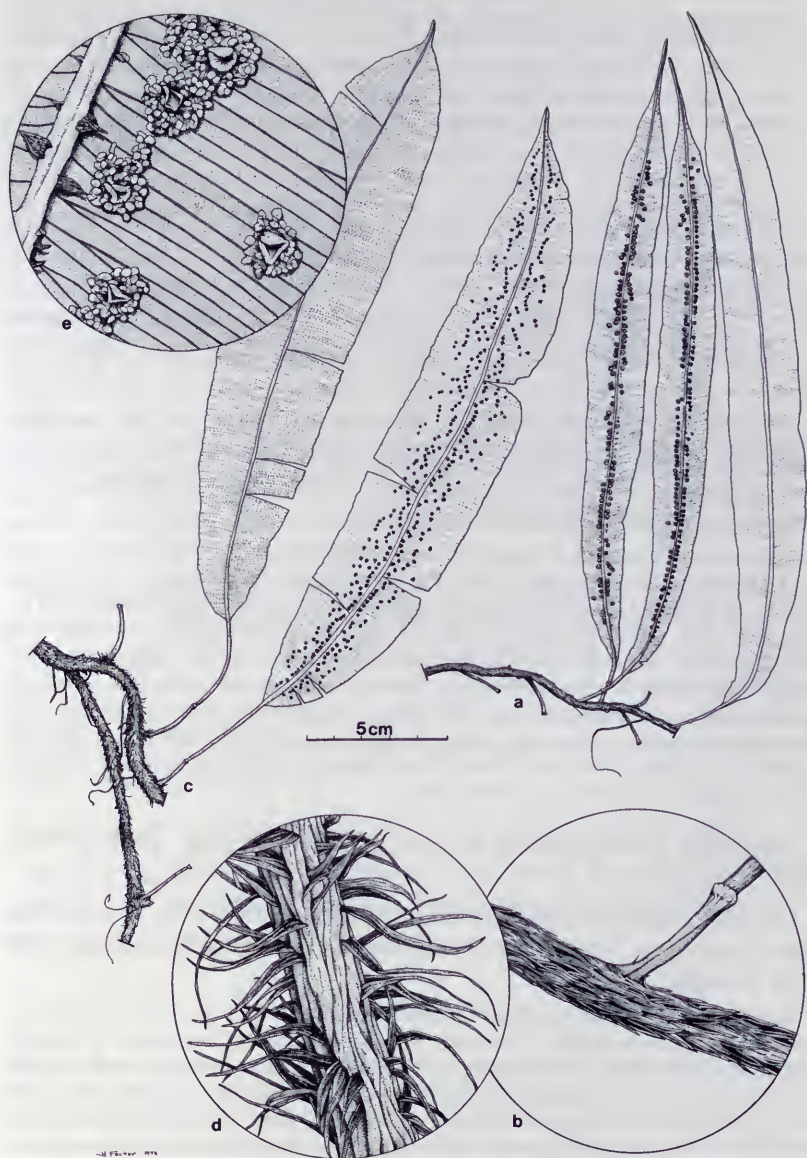


FIG. 52. *Oleandra*. a-b, *O. guatemalensis*: a, habit, $\times \frac{1}{2}$; b, portion of rhizome, showing scales, phyllopodium and articulation, $\times 3\frac{1}{2}$; c-e, *O. articulata*: c, habit, $\times \frac{1}{2}$; d, portion of rhizome with scales, $\times 6\frac{1}{2}$; e, portion of fertile lamina, $\times 6\frac{1}{2}$.

- a. Rhizome scales spreading, essentially concolorous (though sometimes darker at very base); petiole (2) 5-22 cm. long above the phyllopodium; sori in several irregular rows, often extending halfway to the margin. *O. articulata*.
- a. Rhizome scales firmly appressed, bicolorous (lustrous, castaneous to blackish, with light-brown or scarious margins); petiole 0-4 cm. long above the phyllopodium; sori commonly in a single (rarely partially double) row on each side of (and very near) the costa. *O. guatemalensis*.

Oleandra articulata (Sw.) Presl, Tent. Pterid. 78. 1836. *Aspidium articulatum* Sw. J. Bot. (Schrader) 1800 (2): 30. 1801 (type: Plumier t. 136 from Traite Foug. Am. 1705). *Polypodium articulatum* Poir. in Lam. Encycl. 5: 514. 1804. p.p. (not Desv. 1827). *Aspidium nodosum* Willd. Sp. Pl. 5: 211. 1810. *O. nodosa* (Willd.) Presl, Tent. Pterid. 78. 1836.

On tree trunks and stumps, often in swamps, 40-750 m.; Alta Verapaz; Izabal. Southern Mexico (Chiapas); British Honduras; Honduras; Nicaragua; Costa Rica; Panama; West Indies; Colombia to the Guianas, south to Brazil and Bolivia.

Rhizome wide-creeping to scandent, densely provided with linear, filiform-tipped, scales, these spreading, orange to red- or gray-brown, sometimes nearly blackish at the very base, 4-6 mm. long, minutely glandular-ciliate along the margin; leaves to 80 cm. long and 7 cm. broad; phyllopodia widely spaced along the rhizome, 0.5-6 cm. long, scaleless except sometimes at the very base; petiole (2) 5-22 cm. long; lamina firm-herbaceous, elliptic- or oblong-lanceolate, broadly to sharply cuneate at base, acuminate to caudate at apex, lustrous (at least adaxially); costa sparsely to amply scaly abaxially, the scales orange to castaneous, ovate to lanceolate, often filiform-tipped, the base cordate to subpeltate, margins subentire; sori borne in several irregular rows, from the costa to more than halfway to lamina margin.

Oleandra guatemalensis Maxon, Contr. U.S. Natl. Herb. 17: 395. 1914.

On tree trunks or rocky banks in forests, 1,300-1,600 m. Alta Verapaz (type from "trail from Senahú to Actalá," Maxon & Hay 3333); Baja Verapaz. Haiti.

Rhizome wide-creeping to scandent, densely provided with lanceolate to ovate, attenuate scales, these tightly appressed, bicolorous (lustrous, castaneous to blackish, with light-brown or scarious margins), 2-5 cm. long, often with ciliate margins; leaves 10-40 cm. long, 1.5-3 cm. broad; phyllopodia widely spaced on the rhizome, 0.5-2.5 cm. long, scaleless except sometimes at the very base; petiole 0-4 cm. long; lamina firm-herbaceous, linear-elliptic, narrowly cuneate at base, caudate at apex, somewhat lustrous adaxially; costa sparsely scaly abaxially, the scales orange to castaneous, circular to ovate or deltoid-ovate, the base cordate to subpeltate, margins entire or minutely glandular-ciliate; sori borne usually in a single (rarely partially double) row on each side of, and very near, the costa.

ONOCLEOPSIS Ballard

REFERENCE: F. Ballard, A new fern genus from Mexico and Guatemala, Amer. Fern J. 35: 1. 1945.

Plants terrestrial, in wet places; rhizome stout, erect or suberect, to 50 cm. long, abundantly provided with ovate to lanceolate, acuminate, lustrous, light-brown scales; leaves dimorphous, to about 2 m. long (fertile ones shorter); petiole to about 35 cm. long (fertile ones to about 50 cm.), not articulate, light brown or stramineous, smooth-surfaced, provided with scattered scales as on the rhizome; lamina of sterile leaf firm-membranaceous to chartaceous, pinnate to pinnate-pinnatisect, elliptic, narrowing gradually to a pinnatifid apex, reduced somewhat at base; rachis indument and color like that of the petiole; sterile pinnae to 20 cm. long and 3.5 cm. broad, sessile, lanceolate, the apex acuminate, the base truncate or subcordate, subentire to crenate to deeply pinnatisect, the margin broadly serrate, glabrous adaxially, the costae and veins short-pilose or glabrescent abaxially; veins copiously anastomosing, with no included free veinlets; fertile leaves glabrous, or short-pilose on the rachis, 3-pinnate to 3-pinnate-pinnatisect, scarcely foliaceous, laminar tissue commonly limited to the greatly constricted ultimate segments, or to narrow wings along secondary and tertiary axes, each of the ultimate segments bearing (often partially enfolding) a pair of sori abaxially on the veins; sori with indusia essentially lacking, or vestigial as a minute scale; sporangia with long, filiform stalks; spores monolet, biconvex, with perine, golden to dark brown, surface slightly and irregularly verrucose.

This monotypic genus is represented in herbaria by relatively few specimens. Its affinities are with the temperate zone genera *Onoclea* and *Matteuccia*. There has been some confusion as to the color of the spores, for Ballard originally described them as green, and Copeland (Genera Filicum, 1947), observing a single specimen, described them as black. In all the specimens I have examined the spores range from golden brown to dark brown.

Onocleopsis hintonii F. Ballard, Amer. Fern J. 35: 1. 1945.

Growing in wet places in ravines, and along streams and below waterfalls, 1,300-2,800 m.; Jalapa; San Marcos. Southern Mexico.

Characters are those of the genus.

PALTONIUM Presl

Plants small to medium-sized, epiphytic; rhizome thick, short-creeping, densely covered with hairy roots, scaly (especially around petiole bases), the scales rigid, black or blackish brown, or faintly bicolorous, linear-lanceolate to ovate, rather thick, 1-2 mm. long; leaves essentially monomorphic (although tips of fertile ones often somewhat constricted), erect to pendent, crowded, 15-45 cm. long, 1-3 cm. broad, simple linear or narrow-elliptic, entire, short-stalked; petiole 0.5-4 cm. long, stout, terete abaxially, flattened or shallow-sulcate adaxially, glabrous, yellowish brown to castaneous, articulate to the rhizome; lamina opaque, glabrous, coriaceous, commonly tapering subequally



FIG. 53. *Onocleopsis hintonii*. a, rhizome and portion of typical sterile leaf, $\times \frac{1}{2}$; b, portion of sterile pinna, $\times 1\frac{1}{2}$; c, several sterile pinnae, deeply dissected, $\times \frac{1}{2}$; d, fertile pinnae, $\times \frac{1}{2}$; e, apex of fertile pinnule, greatly magnified.

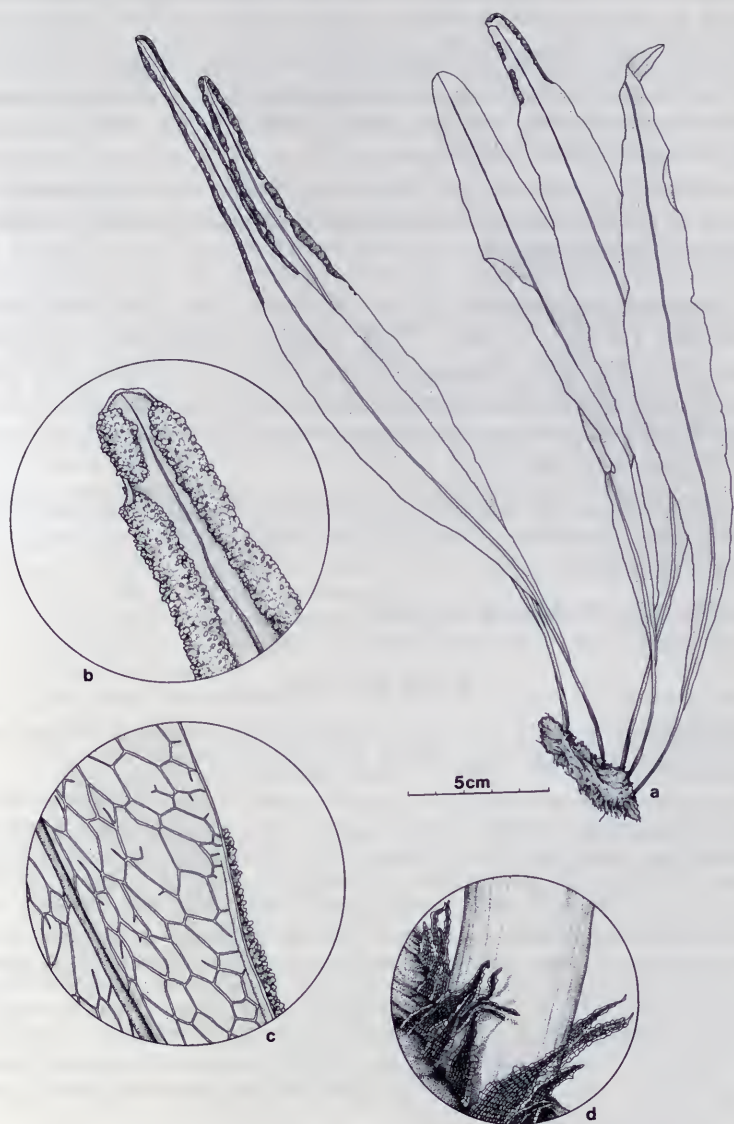


FIG. 54. *Paltonium lanceolatum*. a, habit, $\times \frac{1}{2}$; b, apex of fertile leaf, $\times 3\frac{1}{2}$; c, portion of fertile adaxial side, cleared to show venation, with sporangia projecting from around the margin, $\times 3\frac{1}{2}$; d, scales at petiole base, $\times 13$.

to apex and base, subacute to (mostly) obtuse, margins cartilaginous, often slightly and irregularly undulate, the costa prominulous and distinct nearly to apex, terete abaxially, flattened and usually angular adaxially; venation areolate, indistinct to obscure, the areoles of irregular shape and size, with simple or forked, included, free veinlets; sporangia with long, thin stalks, borne in a rather broad, submarginal, continuous or interrupted soral line toward the apex of, and along each edge of, the lamina; indusium lacking; paraphyses usually numerous, tawny to reddish brown, filamentous; spores monolete, bilateral, without perine.

Paltonium is a monotypic American genus, occurring mainly on islands of the Caribbean Sea, but also infrequently found scattered along or near its coasts.

Paltonium lanceolatum (L.) Presl, Epim. Bot. 156. 1851. *Pteris lanceolata* L. Sp. Pl. 1073. 1753. *Taenitis lanceolata* (L.) Kaulf. Enum. Fil. 130. 1824. *Pteropsis lanceolata* (L.) Fée, Mém. Soc. Linn. Paris 6: 218. 1827. *Neurodium lanceolatum* (L.) Fée, Mém. Fam. Foug. 3: 28. 1852. *Heteropteris lanceolata* (L.) Diels in Engl. & Prantl, Nat. Pflanz. 1 (4): 305. 1899.

In wet forests, not common, on tree trunks, sea level to 200 m.; Izabal; Petén. Southern Florida; West Indies; British Honduras; Honduras; Costa Rica.

Characters are those of the genus.

PELLAEA Link

REFERENCE: A. F. Tryon, A revision of the fern genus *Pellaea* section *Pellaea*, Ann. Mo. Bot. Gard. 44: 129-193. 1957.

Plants terrestrial or, more commonly, epipetric; rhizome short-creeping to decumbent or erect, scaly; leaves essentially monomorphic, short- to long-petiolate, of small to moderate size; petiole not articulate, terete, scaly or pubescent, but more commonly glabrous; lamina pinnate to 3- (4-) pinnate, tapered gradually to a pinnatifid apex or terminating in a discrete, conform, apical segment, not farinose; rachis terete, or adaxially sulcate, glabrous to somewhat pubescent, rarely scaly; pinnae several to numerous, subequilateral, or in some species the basal pair inequilateral (much more strongly produced basiscopically at base); ultimate segments not or scarcely pubescent or scaly (except amply so in *P. rigida*), never beadlike; veins free, mostly forked; indusium continuous, consisting of the strongly revolute, scarcely modified segment margins (but young plants of *P. skinneri* may have greatly modified, sometimes interrupted indusia); sporangia stalked, borne at the tips or apical portion of veins; paraphyses lacking; spores trilete, globose-tetrahedral, with perine.

A number of species of *Pellaea* might appear to fall as logically within the classification of *Notholaena*, or of *Cheilanthes*, for the traditional lines of delimitation of the three genera (according to all previous authors) are not clear. In Guatemala, *P. rigida* and *P. skinneri*

could as well be placed in *Cheilanthes* and *P. formosa* in *Notholaena*. For a more complete discussion of the problems, see treatment of *Cheilanthes*.

About 80 species have been recognized in *Pellaea*, from temperate to tropic regions in both hemispheres, but the greatest concentration is in the New World. The ferns thrive well in xeric habitats and are commonly found on rocks or rocky ground. The following species occur in Guatemala.

- a. Petiole and rachis stramineous, or dull yellowish or grayish brown.
 - b. Pinnae (at least basal ones) inequilateral at base, more strongly produced basiscopically; lamina and each of the pinnae gradually reduced to a nonconform, pinnatifid apex. *P. skinneri*.
 - b. Pinnae subequilateral at base; lamina and each of the pinnae terminating in a discrete, stalked, conform apical segment.
 - c. Rhizome scales bicolorous; costae and (usually) the rachis puberulent (rarely glabrate) and flexuous; pinnae retrorse to (occasionally) spreading. . *P. ovata*.
 - c. Rhizome scales concolorous; costae and rachis glabrous, essentially straight; pinnae ascending to (occasionally) spreading. *P. sagittata*.
- a. Petiole and rachis castaneous to atropurpureous or blackish, lustrous.
 - d. Lamina 3- to 4-pinnate; pinnae conspicuously stalked; ultimate segments 0.3-0.6 cm. long, most of them conspicuously stalked. *P. formosa*.
 - d. Lamina 1- to 2-pinnate; pinnae sessile to short-stalked; ultimate segments (0.5) 0.7-7 cm. long, sessile to short-stalked.
 - e. Rachis amply scaly; lamina gradually reduced to a pinnatifid apex. . *P. rigida*.
 - e. Rachis glabrous to pubescent, not scaly; lamina terminating in a discrete, conform, apical segment.
 - f. Rhizome scales concolorous; pinnae (at least proximal ones) with 1-3 pairs of pinnules and a distinct costa. *P. atropurpurea*.
 - f. Rhizome scales bicolorous, with a sclerotic median stripe; pinnae (most of them) ternate, lacking a distinct costa. *P. ternifolia*.

***Pellaea atropurpurea* (L.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841.**
Pteris atropurpurea L. Sp. Pl. 1076. 1753. *Notholaena atropurpurea* (L.) Keyserl. Polypod. et Cyath. Herb. Bung. 30. 1873.

On shaded or open rocky cliffs, masonry walls, or rocky slopes, 1,800-2,400 m.; Huehuetenango. Mexico; United States; Canada.

Plants epipetric or sometimes terrestrial; rhizome short, decumbent, abundantly scaly, the scales 3-5 mm. long, linear, hair-tipped, concolorous, ferruginous, subentire; leaves numerous, approximate to crowded, erect, 10-50 cm. long, 2-12 cm. broad, petiole; petiole 2-20 cm. long, commonly much shorter than the lamina, lustrous, castaneous, atropurpureous or blackish, terete, scaly at base, sparsely to amply provided with orange to ferruginous, long, fine, mostly appressed trichomes; lamina pinnate or 2-pinnate, chartaceous or subcoriaceous, elongate-triangular, terminating in a discrete, conform, apical segment; rachis terete, lustrous, atropurpureous or blackish, pubescent as on the petiole; pinnae 4-12 pairs, simple and entire or with 1-3 pairs of pinnules, spreading to ascending, short-stalked, or sessile distally, costae pubescent or glabrate;

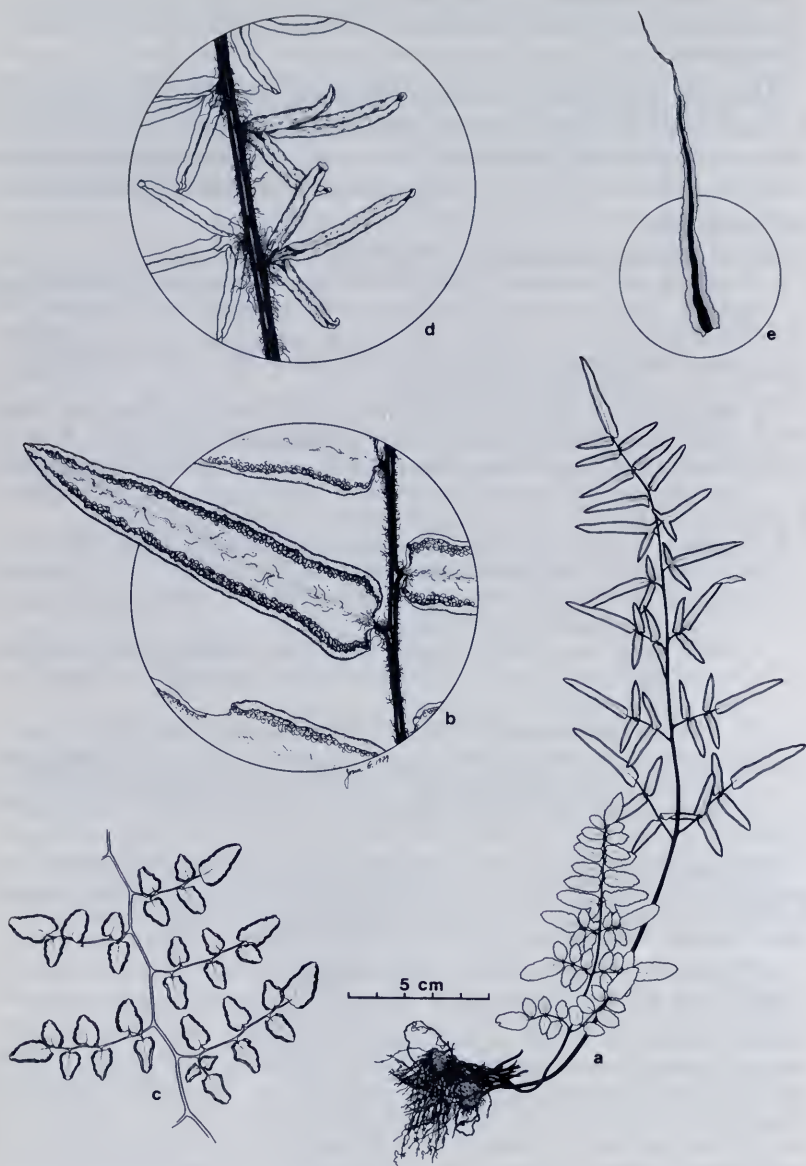


FIG. 55. *Pellaea*. a-b, *P. atropurpurea*: a, habit, $\times \frac{1}{2}$; b, fertile pinnae, $\times 3$; c, *P. ovata*, portion of fertile lamina, $\times \frac{1}{2}$; d-e, *P. ternifolia*: d, rachis and fertile pinnae, $\times 3$; e, rhizome scale, $\times 12\frac{1}{2}$.

ultimate segments 1-7 cm. long, 0.5-1 cm. broad, oblong-lanceolate or linear, subsessile to short-stalked, not adnate, obtuse to acute, often mucronate, truncate, or cordate at base, glabrous, or sparsely appressed-pubescent abaxially; veins commonly 1-forked, obscure, or indistinct abaxially; sori commonly extending the length of the segment from base to tip; indusium formed by the revolute, scarcely to slightly modified segment margin.

Pellaea formosa (Liebm.) Maxon, Contr. U.S. Natl. Herb. 24: 61. 1922. *Allosorus pulchellus* M. & G. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 47. 1842 (not *A. pulchellus* Presl, 1836). *A. formosus* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 220 (seors. 68). 1849. *P. pulchella* (M. & G.) Fée, Mém. Fam Foug. V. (Gen. Fil.): 129. 1850-52. *Notholaena formosa* (Liebm.) Tryon, Contr. Gray Herb. 176: 99. 1956.

In forests or thickets, or in exposed locations, on hillsides, river banks, or, more commonly, on rocks or rocky crevices of cliffs, 1,750-2,100 m.; Huehuetenango. Mexico.

Plants terrestrial or, more commonly, epipetric; rhizome short-creeping, abundantly scaly, the scales 3-6 mm. long, linear to lanceolate, hair-tipped, concolorous, brown or ferruginous, the margins subentire; leaves numerous, caespitose or subcaespitose, 10-30 cm. long, 2-7 cm. broad, petiolate; petiole 3-12 cm. long, equaling, or shorter than the lamina, sublustrous (but often glaucous) castaneous to atropurpureous, terete, glabrous, scaly at base; lamina commonly 3-pinnate, or 4-pinnate at base, lanceolate to deltoid-ovate, chartaceous to subcoriaceous, gradually tapering to a stalked, discrete apical segment similar to the other ultimate segments; rachis terete, castaneous or atropurpureous; pinnae 6-9 pairs, stalked, equilateral at base, ascending; ultimate segments 3-6 mm. long, elliptic or deltoid-oblong, commonly obtuse, stalked, articulate at the stalk, glabrous, sometimes glaucous, the margins revolute, often so strongly that they touch each other on the abaxial side; veins 1- to 2-forked, distinct or indistinct; sori extending from base of segment nearly to the tip, indusium formed by the revolute, scarcely (or not at all) modified segment margin.

This is one of the problem species which stand intermediate between two genera. Tryon removed it from *Pellaea* in his revision of *Notholaena* (1956), but I prefer to maintain it in *Pellaea*, at least until a fully comprehensive study is undertaken of these genera and *Cheilanthes*, and their limits properly set, or all of them merged. I feel it fits much better, *especially* with Guatemalan species, into the (perhaps arbitrary) limits of *Pellaea*: lamina glabrous or sparsely scaly or pubescent, not farinose, the fertile segment margins revolute and continuous, not or scarcely modified; rather than those of *Notholaena*: lamina farinose, or if not, then amply to abundantly scaly or pubescent, the fertile segment margins rarely revolute and continuous, modified or not.

Pellaea ovata (Desv.) Weath. Contr. Gray Herb. 114: 34. 1936. *Pteris ovata* Desv. Mém. Soc. Linn. Paris 6: 301. 1827. *Pteris flexuosa* Klf. ex Schlecht. & Cham. Linnaea 5: 614. 1830. *Pellaea flexuosa* (Klf. ex Schlecht. & Cham.) Link, Fil. Sp. Hort. Bot. Berol. 60: 1841.

In forests, thickets, or wooded ravines, on clay or rocky banks, often on rocks or in crevices of rocky cliffs, 1,300-2,300 m.; Chiquimula; Huehuetenango; Jalapa; Jutiapa; Quezaltenango; El Quiché; Sacatepéquez; Sololá. United States (Texas); Hispaniola; Mexico; Honduras; Nicaragua; Costa Rica; Colombia; Venezuela; Ecuador; Peru; Bolivia; Argentina.

Plants terrestrial or epipetric; rhizome slender, short-creeping, dichotomously branched, with a dense matting of roots, amply scaly, the scales 2-3 mm. long, linear or lanceolate, filiform-tipped, bicolorous, lustrous-castaneous to blackish with a narrow, tawny, often sparsely denticulate margin; leaves rather numerous, approximate to crowded, erect to subscandent, or pendent from banks or cliffs, 15-120 cm. long, 6-20 cm. broad, petiolate; petiole 8-25 cm. long, as long as to (commonly) much shorter than the lamina, stramineous to grayish brown, terete, sparsely arachnoid-pubescent or glabrate, sparsely scaly at base; lamina 2- to 3- (4-) pinnate, chartaceous or subcoriaceous, elongate-triangular, terminating in a discrete, stalked, conform, apical segment; rachis terete, stramineous to gray-brown, densely to sparsely puberulent or glabrate, commonly strongly flexuous; pinnae 15 to many, spreading to (most commonly) retrorse, all of them stalked, elongate-triangular, subequilateral, the costae usually flexuous and densely puberulent, with stout, spreading, minute trichomes; pinnules stalked, simple to pinnate; ultimate segments 0.5-4.5 cm. long, 0.3-2.5 cm. broad, triangular-ovate, cordate or sagittate, obtuse to subacute, sparsely appressed-pubescent or glabrate; veins 1- to 2-forked, these and the segment midrib immersed, obscure; sori often extending nearly the length of the ultimate segments, but commonly terminating just short of the apex and base; indusium formed by the revolute, scarcely modified segment margin.

Pellaea rigida (Sw.) Hook. Sp. Fil. 2: 144. 1858. *Pteris rigida* Sw. Syn. Fil. 104, 299. 1806. *Cheiloplecton rigidum* (Sw.) Fée, Mém. Fam. Foug. 7: 34. 1857. *Cheilanthes rigida* (Sw.) Mett. Abh. Senckenberg Naturf. Ges. 3 (1): 48. 1859 (not Moore, 1861, nor Domin, 1915). *Doryopteris rigida* (Sw.) Diels, Nat. Pflanz. 1 (4): 269. 1899.

On shaded or open clay or rocky banks, on rock outcrops or crevices of cliffs, 800-2,100 m.; Chiquimula; Guatemala; Huehuetenango; Jalapa. Mexico.

Plants epipetric or sometimes terrestrial; rhizome stout, ascending or erect, scaly, the scales light brown to castaneous or blackish, concolorous, linear or linear-lanceolate, entire; leaves numerous, densely crowded, often caespitose, erect, 10-30 cm. long, 4-12 cm. broad, petiolate; petiole 3-12 cm. long, shorter than the lamina, lustrous, castaneous, atropurpureous or blackish, terete, or flattened to shallow-sulcate adaxially near the lamina, rather abundantly provided with tawny to dark-brown, spreading scales, these reduced to and intermixed with subappressed, pluricellular trichomes; lamina pinnate-pinnatisect, subcoriaceous, deltoid or deltoid-ovate, gradually tapering to a pinatifid apex; rachis amply scaly and (usually) pubescent, sulcate adaxially, the ridges

rounded, light colored, and herbaceous; pinnae sessile, 5-10 pairs, proximal ones cut nearly to the base, with the segments lobed to entire and joined by a narrow to broad wing, distal ones entire or with a few basal lobes, basal ones opposite or subopposite, often inequilateral (more strongly produced basiscopically); ultimate segments 0.5-2 cm. long, subtriangular, obtuse to acute, adnate, sparsely to amply scaly and/or pubescent abaxially, pilose (at least near the margins) adaxially; veins distinct to indistinct, pinately arranged along the midrib, commonly 1-forked; sori commonly extending along each margin, from base to tip of segment; indusium formed by the strongly revolute, scarcely to slightly modified segment margin.

This is another species which appears to be intermediate between *Cheilanthes* and *Pellaea*. The segment margins are occasionally somewhat more modified than in typical *Pellaea*, and the surfaces are amply to abundantly scaly and/or pubescent. This and *P. skinneri* seem to serve as stepping stones, bridging the gap between the two genera.

***Pellaea sagittata* (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 60. 1841.**
Pteris sagittata Cav. Descr. Pl. 267. 1802.

On clay or grassy banks, open or shaded, sometimes on rocks, 900-2,400 m.; Huehuetenango; Quezaltenango; Sacatepéquez; Santa Rosa; Sololá. Mexico; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Plants terrestrial, often epipetric; rhizome erect to ascending, amply scaly, the scales 2-4 mm. long, flaccid, lanceolate to ovate, dull, concolorous, tawny or orange, the margins denticulate; leaves rather numerous, crowded to subfasciculate, erect (at least in ours), 15-70 cm. long, 4-24 cm. broad, petiolate; petiole 8-20 cm. long, equaling or shorter than the lamina, stramineous to reddish brown, terete; or slightly flattened adaxially, sparsely arachnoid-pubescent or glabrate, sparsely to amply provided with tawny scales, especially at base; lamina commonly 2-pinnate, chartaceous to subcoriaceous, elongate-triangular or subrhomboid, terminating in a discrete, stalked, conform, apical segment; rachis terete, stramineous to reddish brown, essentially glabrous (in ours) but often sparsely or amply provided with tawny or whitish scales, straight (not flexuous); pinnae 6-12 pairs, ascending (in ours), all of them stalked, elongate-triangular, subequilateral, the costae straight, glabrous (in ours); ultimate segments stalked, to 5.5 cm. long and 3 cm. broad, circular and cordate or (as in ours) elongate-triangular and sagittate, obtuse to subacute, glabrous, margins revolute; veins 2- to 3-forked, distinct, at least abaxially; sori extending nearly or quite to the tips of the ultimate segments; indusium slightly thinner than the leaf tissue, equal or lighter in color.

Ours is the typical variety of the species. *Pellaea sagittata* var. *cordata* (Cav.) A. F. Tryon is found from Texas to Oaxaca, Mexico, and differs chiefly in having longer, lax or spreading leaves, with puberulent rachis and costae, spreading (rather than ascending) pinnae, and circular and cordate ultimate segments.

***Pellaea skinneri* Hook. Sp. Fil. 2: 141, t. 118b. 1858** (type from Guatemala, location unspecified, *Skinner s.n.*). *Cheilanthes skinneri*

(Hook.) Moore, Index Fil. 253. 1861. *Doryopteris skinneri* (Hook.) C. Chr. Index Fil. 245. 1905.

On banks of ravines, or on wooded slopes or cliffs, 200-1,400 m.; Chiquimula; Zacapa. Mexico; El Salvador; Nicaragua; Costa Rica.

Plants terrestrial; rhizome short, erect or ascending, with roots dense and spreading, amply scaly, the scales 1-2 mm. long, linear, most of them bicolorous, lustrous-castaneous to blackish, with a narrow, orange or light-brown margin; leaves few, erect, crowded, 20-70 cm. long, 7-22 cm. broad, petiolate; petiole 10-40 cm. long, equaling or somewhat shorter than the lamina, stramineous to grayish brown, subterete, slightly flattened adaxially, pale- and filiform-scaly, but the scales more numerous and darker or bicolorous at petiole base; lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatifid, thin-herbaceous to chartaceous, deltoid, tapering to a gradually pinnatifid apex, sparsely pubescent or pubescent-scaly or glabrate; rachis stramineous to grayish brown, subterete, slightly flattened or shallowly sulcate adaxially, sparsely pubescent or pubescent-scaly; pinnae 3-10 pairs, ascending, stalked, but becoming sessile distally, deltoid, tapering gradually to a pinnatifid apex, most of them (or at least the basal pair) inequilateral at base, more strongly produced basiscopically; pinnules adnate, or the largest ones stalked, lobed to pinnate-pinnatifid; ultimate segments acute, lanceolate- to deltoid-ovate; veins distinct, 1- to several-forked; sori elongated (occasionally short and discrete), but not reaching the tips or sinus of ultimate segments; indusium at first strongly reflexed, spreading at maturity, thin, yellow or greenish (or sometimes scarious in young plants), subentire to irregularly erose or undulate.

It is with great reluctance that I maintain this species in *Pellaea*. The laminae of some plants examined are more than just sparsely pubescent and scaly, and indusia are occasionally quite short, flaplike, and nearly scarious when young. (The latter closely resemble indusia of some species of *Hypolepis*.) According to definition of terms used in this treatment, *P. skinneri* could as well be placed in *Cheilanthes*, and serves as one of a number of examples why these generic concepts are in urgent need of reassessment.

Pellaea ternifolia (Cav.) Link, Fil. Sp. Hort. Bot. Berol. 59. 1841. *Pteris ternifolia* Cav. Descr. Pl. 266. 1802. *Cheilanthes ternifolia* (Cav.) Moore, Index Fil. 255. 1861. *Nothochlaena ternifolia* (Cav.) Keyserl. Polypod. et Cyath. Herb. Bung. 29. 1873.

In shaded or exposed situations, on clay banks or ridges, but more commonly on rocky slopes, rock outcrops, or lava flows, 1,800-2,500 m.; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Quezaltenango; Sololá. Mexico; El Salvador; Nicaragua; southwestern United States; Dominican Republic; Colombia and Venezuela southward to Chile and Argentina; Hawaiian Islands.

Plants epipetric or sometimes terrestrial; rhizome short, decumbent, abundantly scaly, the scales 4-5 mm. long, linear, hair-tipped, bicolorous, tawny to orange, with a lustrous, castaneous to blackish median stripe, the margins more or less denticulate; leaves numerous, crowded to subfasciculate, erect and rigid, 8-40 cm. long, 1.5-5 cm.

broad, petiolate; petiole 3-18 cm. long, shorter than the lamina, lustrous (but often glaucous) castaneous to atropurpureous or blackish, terete, but commonly flattened to shallow-sulcate adaxially, scaly at base, the scales concolorous or bicolorous, glabrous above, or sometimes sparsely fine-pubescent; lamina simply pinnate to pinnate-pinnatifid (in ours), subcoriaceous, terminating in a discrete, conform, apical segment; rachis flattened to sulcate adaxially, castaneous to atropurpureous or blackish; pinnae 5-15 pairs, (in ours) simple or ternate and sessile or subsessile; ultimate segments (0.5) 0.7-2 cm. long, 0.1-0.5 cm. broad, linear-lanceolate to oblanceolate, sessile or subsessile, not adnate, acute to (more commonly) mucronate, typically the margins so strongly revolute that they touch on the abaxial side, essentially glabrous; veins commonly 1-forked, obscure; sori extending from base of segment nearly to the mucronate tip, indusium formed by the revolute, scarcely modified segment margin.

In Guatemala, *P. ternifolia* is represented by the typical variety. In the southwestern United States and adjacent Mexico is found var. *wrightiana* (Hook.) A. F. Tryon, which has the lower pinnae each divided into 1-5 pairs of pinnules, with a definite costa, and the rhizome scales with a much broader, sclerotic median stripe.

PELTAPTERIS Link

REFERENCE: C. V. Morton, Notes on *Elaphoglossum*, III: The publication of *Elaphoglossum* & *Rhipidopteris*, Amer. Fern J. 45: 11-14. 1955.

Plants small, epiphytic; rhizome creeping, slender, scaly; leaves dimorphous, 2-10 (12) cm. long, 0.5-5 cm. broad, widely spaced, long-petiolate; petiole not articulate at the rhizome, sparsely to amply scaly; sterile lamina flabellate and deeply, dichotomously dissected (in ours), subentire, or (in *P. peruviana* Gomez) deeply pinnatifid, firm-herbaceous, essentially glabrous, but commonly with scattered, peltate scales on either surface; veins free; fertile lamina much smaller than the sterile, many times shorter than the petiole, irregularly circular, cordate or obcordate, subentire, erose, crenulate or lobed, completely covered with sporangia on the abaxial surface; indusia and paraphyses lacking; spores monolete, reniform to elliptic, with perine.

The taxonomy and nomenclature of the genus had been greatly confused in the past, but thanks to Morton (1955) most of the problems have been solved.

Peltapteris is closely related to *Elaphoglossum*, but is distinguished from the latter chiefly by the deeply dissected sterile lamina. It is a neotropical genus of 3 or 4 species, which has been often subdivided into a number of varieties or forms by various authors. A single species is recognized in Guatemala.

Peltapteris peltata (Sw.) Morton, Amer. Fern J. 45: 13. 1955. *Os-munda peltata* Sw. Nov. Gen. Sp. Pl. Prodr. 137. 1788. *Acrostichum peltatum* (Sw.) Sw. J. Bot. (Schrader) 1800 (2): 11. 1801. *Rhipidopteris*

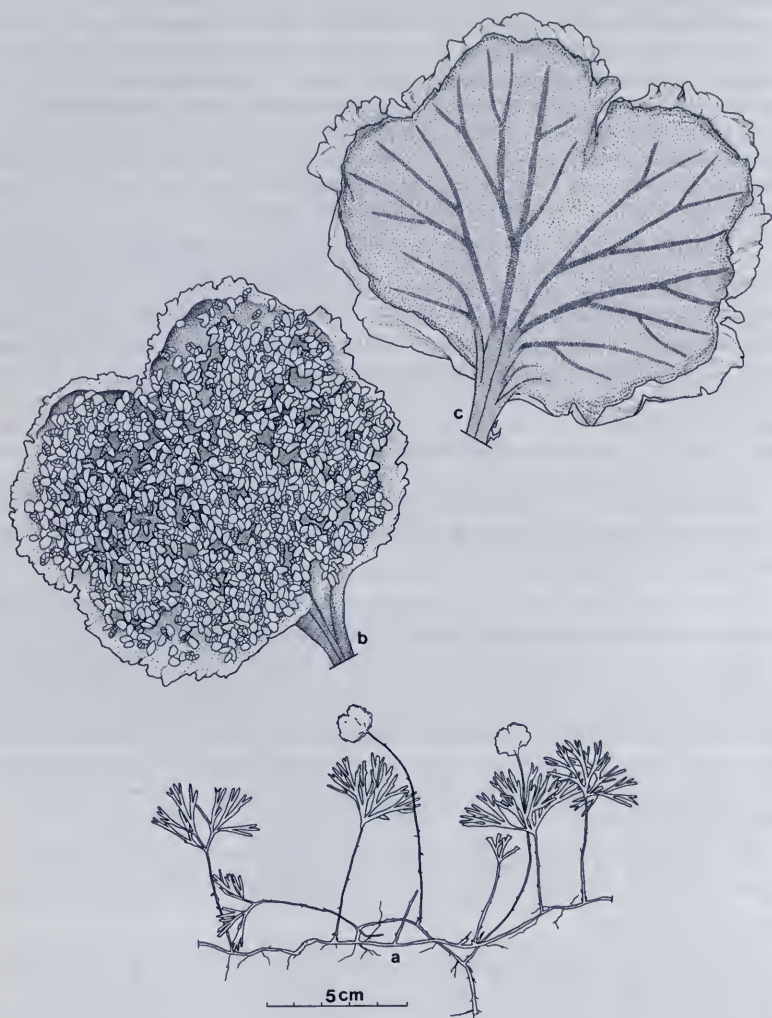


FIG. 56. *Peltapteris peltata*. a, habit, with sterile and fertile leaves, $\times \frac{1}{2}$; b, fertile lamina, abaxial surface, $\times 6$; c, fertile lamina, adaxial surface, cleared to show venation, $\times 6$.

peltata (Sw.) Schott ex Fée, Mém. Fam. Foug. 2: 14. 1845 (*nom. illeg.*). *Elaphoglossum peltatum* (Sw.) Urban, Symb. Antill. 4: 60. 1903.

In wet forests and wooded ravines, on trunks or branches of trees or on rotting logs, 100-2,500 m., Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Guatemala; Huehuetenango; Izabal; Jalapa; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Zacapa. West Indies; southern Mexico to Panama; Colombia; Venezuela; Ecuador; Peru.

Rhizome slender, amply to abundantly provided with flaccid, brown scales, these lanceolate to ovate, 2-4 mm. long. Sterile leaves numerous, 2-10 cm. long; petiole 1-7 cm. long, 1-3 times as long as the lamina; lamina 1-3 cm. long, as broad as or broader than long, flabellate, reniform to circular, deeply and dichotomously dissected, firm-herbaceous, opaque, sparsely scaly, at least abaxially, and often gland-dotted; ultimate segments 0.5-1.5 mm. broad, sparsely provided with minute scales, these light brown to castaneous, ovate to lanceolate or amorphous, peltate, often substellate; veins 1 to a segment, dichotomously branched as the divisions of the lamina branch. Fertile leaves few, interspersed among the sterile, 4-10 cm. long; petiole 3-9 cm. long, many times longer than the lamina; lamina 0.5-1.0 cm. long, as broad as or broader than long, the sporangia covering the entire lamina abaxially, except for a narrow band along the margin.

Various authors have split *P. peltata* into several other species, or varieties or forms, on the basis of the depth of dissection of the sterile lamina. Only one of these, *P. flabellata* (H. & B.) Morton, perhaps merits recognition as a variety. In this, the sterile lamina resembles the fertile in that it is scarcely or not at all dissected. However, this particular variant is not known to occur in Guatemala. Another "variant," *P. peltata* forma *foeniculacea* (Hook. & Grev.) Morton, is supposed to differ from the typical merely in its somewhat smaller sterile leaves and narrower ultimate segments. This condition has been seen to occur in a few populations of Guatemalan plants, but the difference is a purely quantitative one and next to impossible to delimit or describe satisfactorily.

PITYROGRAMMA Link

REFERENCE: R. M. Tryon, The genus *Pityrogramma*, in Taxonomic fern notes II, Contr. Gray Herb. 189: 52-74. 1962.

Plants terrestrial; rhizome small to very stout, erect to ascending, scaly, the scales rather stout, filamentous to (less commonly) relatively broad; leaves essentially monomorphic (or in a few species the fertile lamina with somewhat constricted segments), short- to long-petiolate, erect, densely fasciculate, in ours 0.3-1.6 m. long; petiole not articulate, yellowish brown to, more commonly (as in ours), lustrous and

atropurpureous or blackish, glabrous, but scaly at base; lamina pinnate to 3-pinnate (in *P. trifoliata* 2- or 3-foliolate), firm-herbaceous to subcoriaceous, in most species white- to yellow- or roseate-farinoso abaxially, sometimes pubescent or completely glabrous; pinnae numerous, spreading to ascending, commonly sessile or subsessile; veins free, forked, often indistinct, extending fully to the segment margins; sporangia short-stalked, not arranged in discrete sori, borne abaxially along the veins, mostly near the margin, but at maturity commonly filling the entire segment; indusia lacking, but segment margin often somewhat revolute and partially protecting the sporangia; paraphyses none; spores commonly trilete and globose-tetrahedral, with perine.

Pityrogramma is a genus of small to medium-sized ferns with attractive, bicolorous leaves. The lamina (except sometimes in juvenile or very mature stages) is dark to bright green above, while the segments beneath in most species are covered with a farinose indument ranging in color from chalky white to a reddish or golden yellow. Earlier workers attempted to place greater importance on these colors, but it now appears that they vary too widely (even on the same plant) to be of taxonomic value, at least at the species level.

Approximately 20 species of *Pityrogramma* are found in tropical and subtropical regions around the world, the majority of these occurring in the neotropics. Five have been found in Guatemala.

- a. Pinnae simple, 2-foliolate or 3-foliolate (rarely more than 3-foliolate); larger ultimate segments (pinnae or pinnules) 5-12 cm. long, 8-30 times as long as broad. *P. trifoliata*.
- a. Pinnae pinnatisect to 2-pinnate; larger ultimate segments 1-3 cm. long, 1-4 (-6) times as long as broad.
- b. Lamina densely and persistently lanate abaxially. *P. ferruginea*.
- b. Lamina glabrous, farinose, or sparsely pubescent.
- c. Pinnae (especially proximal ones) inequilateral at base, more strongly produced basiscopically than acroscopically; pinnules spreading nearly at right angles from the costa. *P. tartarea*.
- c. Pinnae subequilateral at base; pinnules sharply ascending, the basal basiscopic ones even more strongly so than the acroscopical ones.
- d. Ultimate segments mostly obovate or oval; lamina (even on smaller leaves) 2-pinnate-pinnatifid, at least as to the proximal pinnae. *P. dealbata*.
- d. Ultimate segments lanceolate, narrow-deltoid, elliptic or oblong; lamina pinnate-pinnatisect to 3-pinnate, but smaller ones mostly only pinnate-pinnatifid. *P. calomelanos*.

***Pityrogramma calomelanos* (L.) Link, Handb. Gewäcse 3: 20. 1833. *Acrostichum calomelanos* L. Sp. Pl. 1072. 1753. *A. ebenum* L. tom. cit. 1071.**

In thickets or damp, wooded ravines or, as often, on open banks or rocky slopes, sea level to 1,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Izabal; Petén; Quezaltenango; El Quiché; Retalhuleu; San Marcos; Santa Rosa; Zacapa. Southern Florida; West Indies; Mexico to Colombia and French Guiana, south to



FIG. 57. *Pityrogramma*. a-b, *P. dealbata*: a, habit, $\times \frac{1}{2}$; b, pinnule, $\times 3$; c, *P. calomelanos*, pinna, $\times \frac{1}{2}$; d, *P. tartarea*, pinna, $\times \frac{1}{2}$; e, *P. trifoliata*, pinna, $\times \frac{1}{2}$; f, *P. ferruginea*, portion of rachis and base of fertile pinna, $\times 6$.

Bolivia, Paraguay, and Argentina; according to Tryon (1962) also widely introduced in the Paleotropics.

Rhizome slender to stout, erect or ascending, amply provided with lustrous, orange to castaneous scales, these linear to filamentous, 2-4 mm. long; leaves to 1 m. long, lanceolate to deltoid-ovate, commonly long-petiolate; petiole wiry to stout, lustrous, castaneous to atropurpureous, terete abaxially, sulcate adaxially, essentially glabrous, but often sparsely ceraceous and scaly at base, the scales like those of the rhizome, but longer and broader; lamina pinnate-pinnatisect to (on larger leaves) 2-pinnate-pinnatifid or nearly 3-pinnate, firm-herbaceous to chartaceous, essentially glabrous adaxially and on the axes, white- or pale yellow-farinose abaxially, slightly or not reduced at base, gradually tapering to a pinnatifid apex; rachis lustrous, sometimes thinly farinose, castaneous to atropurpureous; pinnae commonly ascending, mostly short-stalked, subequilateral; pinnules sharply ascending (the basal basiscopic ones especially so); ultimate segments 3-10 mm. long, 1-3 times as long as broad, lanceolate, narrow-deltoid, elliptic, or oblong, most of them acute, often acutely lobed or sharply serrate; veins distinct to indistinct, 1- or 2-forked.

Tryon (1962) cites two varieties of *P. calomelanos* occurring elsewhere in Central America and in South America, distinguished by the lamina lacking or having differently colored farina. Ours is the typical, most wide-ranging variety.

Pityrogramma dealbata (Presl) Tryon, Contr. Gray Herb. 189: 67. 1962. *Gymnogramma dealbata* Presl, Rel. Haenk. 1: 18, t. 3, f. 1. 1825. *Ceropteris schaffneri* Fée, Mém. Fam. Foug. 8: 80. 1857. *P. schaffneri* (Fée) Weath. Contr. Gray Herb. 114: 25. 1936.

In thickets or shaded ravines, but more often on dry, open banks, 500-2,400 m.; Escuintla; Guatemala; Jutiapa; El Quiché; Sacatepéquez; Santa Rosa. Mexico to Panama.

Rhizome slender to stout, erect or ascending, amply provided with lustrous, orange to castaneous scales, these linear to filamentous and tortuous, 2-3 mm. long; leaves to 60 cm. long, lanceolate to deltoid-ovate, mostly long-petiolate (in larger leaves the petiole about as long as the lamina); petiole wiry to stout, lustrous, castaneous to atropurpureous, terete abaxially, sulcate adaxially, essentially glabrous, but sparsely scaly and often white-farinose at base; lamina 2-pinnate-pinnatifid (at least as to the proximal portion) to nearly 3-pinnate, firm-herbaceous to chartaceous, essentially glabrous adaxially and on the axes, white- to yellow-farinose and (rarely) sparsely pubescent abaxially, slightly or not reduced at base, gradually tapering to a pinnatifid apex; rachis lustrous, sometimes thinly farinose, atropurpureous; pinnae spreading to ascending, sessile to short-stalked, subequilateral; pinnules sharply ascending (the basal basiscopic ones especially so); ultimate segments 2-8 mm. long, 1-2 times as long as broad, most of them obovate or oval; veins distinct to indistinct, 1- or 2-forked.

This may be only a variant of *P. calomelanos*. It is a smaller fern, commonly with more highly dissected lamina, and the ultimate segments are mostly obovate or oval. Laminae of *P. calomelanos* vary in dissection, depending largely on the size of the individual leaf, with ultimate segments also varying in shape; however, the latter are never

obovate or oval as in *P. dealbata*. For purposes of this treatment the two are maintained as separate species, but careful study in the field and in the greenhouse may eventually show them to differ only on an infraspecific level.

Pityrogramma ferruginea (Kunze) Maxon, Contr. U.S. Natl. Herb. 17: 173. 1913. *Gymnogramma ferruginea* Kunze, Linnaea 9: 34. 1834. *G. bommeri* Christ, Bull. Soc. Roy. Bot. Belgique 35: 237. 1896.

Commonly on open banks, often on lava flows of volcano slopes, 1,200-2,000 m.; Escuintla; Suchitepéquez. Honduras to Panama; Peru.

Rhizome stout, densely provided with lustrous, orange, linear scales, these 2-4 mm. long, with filamentous tips; leaves (in ours) to 40 cm. long (elsewhere to nearly 1 m.), elliptic, commonly short-petiolate; petiole stout, lustrous, atropurpureous, terete to somewhat flattened abaxially, sulcate adaxially, densely covered (especially at base) with orange, filamentous scales and tortuous, pluricellular trichomes; lamina commonly pinnate-pinnatisect to nearly 2-pinnate, subcoriaceous, essentially glabrous adaxially, densely lanate on the axes and abaxial surface (so much so that the surface is often obscured), rather strongly reduced at base, gradually tapering to a pinnatifid apex; rachis lustrous, deep-castaneous to atropurpureous; pinnae spreading to ascending, sessile or subsessile, subequilateral, the lobes spreading at broad (often 90°) angles, these mostly obtuse, rarely reaching 1 cm. in length, their margins often strongly revolute; veins indistinct to obscure, commonly 1-forked.

Pityrogramma tartarea (Cav.) Maxon, Contr. U.S. Natl. Herb. 17: 173. 1913. *Acrostichum tartareum* Cav. Descr. Pl. 242. 1802. *Hemionitis dealbata* Willd. Sp. Pl. 5: 131. 1810, *nom. illeg.* *Gymnogramma peruviana* Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 329. 1811. *G. dealbata* Link, Hort. Reg. Bot. Berol. 2: 52. 1833, *nom. illeg.* (not Presl, 1825). *P. peruviana* (Desv.) Maxon, Contr. U.S. Natl. Herb. 17: 173. 1913. *P. calomelanos* var. *peruviana* (Desv.) Farw. Amer. Midl. Naturalist 12: 280. 1931.

In forests, thickets, and wooded ravines, but as often found on open banks, cliffs, and rocky hills, 1,250-2,800 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Suchitepéquez; Totonicapán. Greater Antilles; Mexico to Colombia and Venezuela, south to Bolivia and Brazil.

Rhizome stout, densely provided with lustrous, orange to dark-brown or blackish, linear scales, these 4-10 mm. long, with long, filiform, often deciduous tips; leaves to 1 m. long, lanceolate to deltoid-ovate, short- to long-petiolate; petiole stout, lustrous, castaneous to atropurpureous, terete to slightly flattened or angular abaxially, sulcate adaxially, essentially glabrous, but sparsely to amply scaly at base; lamina pinnate-pinnatifid to (at base) 2-pinnate (or the very large ones nearly 3-pinnate), chartaceous to subcoriaceous, essentially glabrous adaxially and on the axes, white-farinose and (occasionally) sparsely pubescent abaxially, slightly or not reduced at base, gradually taper-

ing to a pinnatifid apex; rachis lustrous, sometimes thinly farinose, atropurpureous; pinnae spreading to ascending, sessile to (proximally) short-stalked, at least the proximal ones strongly inequilateral at base, more strongly produced basiscopically; pinnules spreading at broad (often 90°) angles from the costa; ultimate segments (larger ones) 1-3 cm. long, 2-4 (-6) times as long as broad, obtuse to acute, the margins often strongly revolute; veins indistinct to obscure, often immersed adaxially, commonly 1-forked.

There are perhaps two varieties of *P. tartarea* which occur in South America, distinguished by lack of, or differently colored, farina. Ours, with densely white-farinose abaxial surfaces, is the typical variety.

Pityrogramma trifoliata (L.) Tryon, Contr. Gray Herb. 189: 68. 1962. *Acrostichum trifoliatum* L. Sp. Pl. 1070. 1753. *Trismeria trifoliata* (L.) Diels, Nat. Pflanz. 1(4): 265. 1899.

In wet, often sandy or rocky soil, in thickets, meadows, or along banks of streams or rivers, 200-2,300 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Quezaltenango; Retalhuleu; San Marcos; Santa Rosa; Sololá; Zacapa. Southern Florida; Greater Antilles; Mexico to Costa Rica; Colombia and Venezuela south to Argentina and Chile.

Rhizome stout, amply provided with linear or lanceolate scales, these 2-3 mm. long, orange to castaneous to dark brown or blackish; leaves to 1.6 m. long, linear-lanceolate to narrow-ovate, commonly short-petiolate; petiole stout, to nearly 1 cm. in diameter, lustrous, castaneous to (more commonly) atropurpureous, terete abaxially, sulcate adaxially, glabrous (distally) to scaly, often densely so at base, the scales similar to those of the rhizome; lamina simply pinnate to 2- or 3-foliolate (rarely to 7-foliolate), chartaceous to subcoriaceous, glabrous adaxially, glabrous to white- or yellow-farinose abaxially, somewhat reduced at base, terminating abruptly in a conform apical segment; rachis lustrous, castaneous to atropurpureous, sulcate adaxially, glabrous to sparsely white-farinose or -scurfy; pinnae sessile to short-stalked, larger ones 5-12 cm. long, simple and linear or linear-lanceolate, or bearing at or near the base 1-2 (-6) similar but somewhat smaller segments (pinnules), these adnate to stalked; ultimate segments (at least the larger ones) 8-30 times longer than broad, regularly and minutely serrate or crenate-serrate, cuneate at base, obtuse to acute at apex, fertile ones often somewhat constricted and revolute, and narrower than the sterile; veins 1-3 times dichotomously branched, the branches running in subparallel fashion to the margin.

PLECOSORUS Fée

REFERENCE: A. L. A. Fée, *Plecosorus* (pp. 150-151) in: Mém. Fam. Foug. 5 (Gen. Fil.): 1-387. 1850-52.

Plants terrestrial, often subarborescent, with a stout, woody caudex to 30 cm. long and 15 cm. in diameter; leaves monomorphous, crowded, rigid, erect, to 90 cm. long and 20 cm. broad, densely scaly, lacking trichomes, but the scales of the secondary and tertiary axes often hairlike; petiole not articulate, 10-25 cm. long, terete to subquadrangular abaxially, canaliculate adaxially, densely covered with tawny, orange, or dark-brown, spreading, scales (sometimes gray-white in age), these commonly 2-4 cm. long,

linear to lanceolate, the margins erose to remotely spinulose-dentate, the tips attenuate; lamina subcoriaceous, 2-pinnate-pinnatifid to 3-pinnate, lanceolate, tapering gradually at both apex and base; rachis densely covered with linear, often hairlike, tawny or orange scales; pinnae numerous, sessile or subsessile, spreading to ascending, or a few proximal pairs deflexed, costae and costules deeply and narrowly sulcate adaxially, densely scaly as on the rachis; pinnules sessile, crowded, obtuse, spreading at right angles to the costa, cut deeply or fully to the costule; ultimate segments obtuse, strongly reflexed, beadlike, frequently subbullate and thoroughly protecting the sporangia as pseudoindusia, the margins scarious, erose to sharply dentate; veins free, pinnate, 1- or 2-forked in the ultimate segments; true indusia lacking; paraphyses lacking; sporangia long-stalked, arranged in indefinite patterns abaxially on the veins, at maturity often completely covering the surface of the segment; spores monolete, biconvex, with thick perine.

Plecosorus is a monotypic genus, very closely related to *Polystichum*, within which Copeland and some others have preferred to include it. *Plecosorus* lacks indusia, although the beadlike segments have their margins so strongly revolute they function as indusia. Typically *Polystichum* has peltate indusia, although in a few species indusia are minute and fugacious or lacking. Ultimate segments in *Polystichum* are spinulose, whereas they are not in *Plecosorus*. Sori are discrete (sometimes confluent at maturity) in *Polystichum*, but sporangia in *Plecosorus* are arranged in indefinite patterns along the veins, and at maturity completely cover the abaxial surface of each fertile segment.

Plecosorus speciosissimus (A. Br.) Moore, Index Fil. XL. 1857. *Cheilanthes speciosissima* A. Br. in Kunze, Anal. Pterid.: 35, t. 23. 1837. *P. mexicanus* Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 151. 1850-52.

In coniferous forests, often on slopes or steep banks, 2,400-4,000 m.; Chimaltenango; Huehuetenango; Quezaltenango; Sacatepéquez; San Marcos; Sololá; Totonicapán. Mexico; Costa Rica; Panama.

Characters are those of the genus.

X PLEURODERRIS Maxon

REFERENCE: W. R. Maxon, *Pleuroderris*, a new genus of Middle American ferns, J. Wash. Acad. Sci. 24: 549-557. 1934.

Plants of medium size, terrestrial, erect; rhizome stout, suberect, provided with dark-brown, lanceolate to ovate, often attenuate scales; leaves caespitose, monomorphous, petiolate, to 1 m. long and 0.3 m. broad; petiole to 40 cm. long, sparsely scaly, yellowish brown to castaneous, commonly lustrous (especially toward the lamina), not articulate; lamina variable, often asymmetrical, shallowly to deeply lobed, or at the base pinnatisect or fully pinnate, broadest at or near the base, tapering to a subentire, usually attenuate apex, firm-herbaceous to chartaceous, glabrous, or sparsely hispidulous on the



rachis adaxially; pinnae (or lobes) obtuse to acuminate, crowded, with narrow, acute sinuses or (especially the proximal ones) subdistant with broadly rounded sinuses; veins copiously anastomosing, catadromous, the areoles commonly including secondary areoles and free veinlets which spread in all directions; sori round or elongated, borne on the veins abaxially, scattered irregularly along or near segment margins; indusium dark brown, lustrous, laterally attached to and conforming to the shape of the sorus, often lobed when elongated; paraphyses lacking; sporangia crowded, long-stalked, mostly abortive; spores few, mostly abortive, oblong, brown, irregularly verrucate or tuberculate.

Copeland (Gen. Fil. 133. 1947) and others have long suspected the hybrid nature of this monotypic genus. Putative parents are *Dictyoxiphium panamense* and *Tectaria* sp., which share the habitat and distribution of *Pleuroderris*. (The genus is discussed in some detail in Wagner, Wagner, and Gómez: Amer. J. Bot. 59: 677. 1972, and Biotropica 10: 254-264. 1978.) Extreme variability in the leaf originally promoted some taxonomic confusion, which resulted in a number of synonyms for the species. The lamina may resemble some species of *Tectaria*, i.e., cleft deeply or fully to the rachis, with broad sinuses between long, attenuate pinnae, and the basal pinnae the longest. At the other extreme, the lamina may be very narrowly lanceolate and deeply cleft only near the base, the central part broadly and shallowly lobed, and the apical section attenuate and subentire like *Dictyoxiphium*. At times the lamina may be quite asymmetrical, with some pinnae or lobes much shorter and broader than those immediately above or opposite. The genus is one of the most unique in Guatemala.

X *Pleuroderris michleriana* (Eaton) Maxon, J. Wash. Acad. Sci. 24: 551. 1934. *Lindsaea michleriana* Eaton, Mem. Amer. Acad. Arts, n.s., 8: 213. 1860. *Dictyoxiphium michlerianum* (Eaton) Moore, Index Fil. 319. 1861. *Hypoderris seemannii* Prentice, J. Bot. 7: 240. 1872. *H. marginalis* Fourn. Bull. Soc. Bot. France 9: 260. 1872. *H. adnata* Fourn. l.c. *Polypodium tatei* Baker in Hook. & Bak. Syn. Fil. 2: 506. 1874. *H. heteroneuroides* Christ, Bull. Herb. Boissier II. 6: 292. 1906 (type from Cubilgüitz, Alta Verapaz, Tuerckheim 8821).

In wet, lowland forests, along streams and rivers and at edges of marshes, 35-300 m.; Alta Verapaz; Izabal. Nicaragua; Costa Rica; Panama; Colombia.

Characters are those of the genus.

Opposite:

FIG. 58. *Plecosorus speciosissimus*. a, habit, $\times \frac{1}{2}$; b, petiole scales, $\times 4$; c, fertile pinnules, $\times 15$.

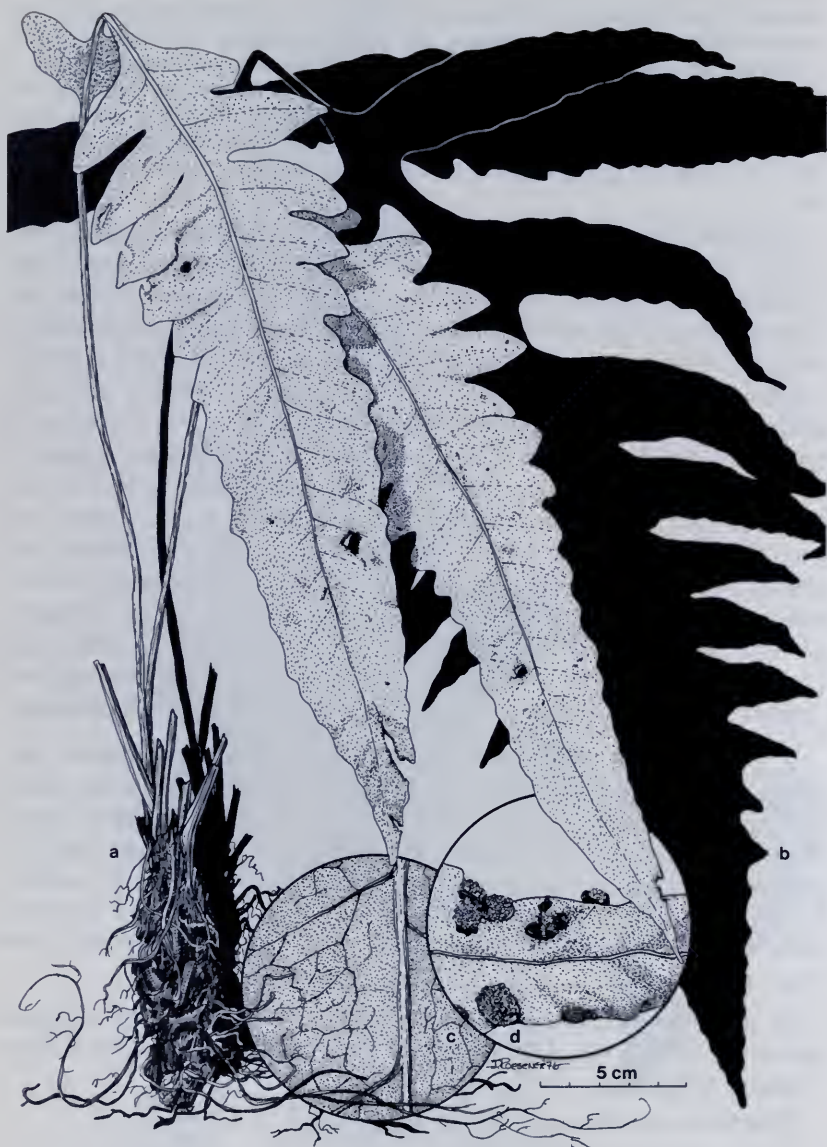


FIG. 59. X *Pleuroderris michleriana*. a, habit, shallow-lobed leaf, $\times \frac{1}{2}$; b, silhouette, pinnatifid leaf, $\times \frac{1}{2}$; c, portion of lamina, showing venation, $\times 2\frac{1}{2}$; d, portion of soriferous segment, $\times 3$.

POLYBOTRYA Humboldt & Bonpland

REFERENCES: A. L. A. Fée, *Polybotrya* (pp. 72-78) in Hist. des Acrost. [Mém. Fam. Foug. 2]: 1-114. 1845. *Olfersia* (pp. 81-82) *loc. cit.* *Soromanes* (p. 82) *loc. cit.*

Plants terrestrial to epiphytic; rhizome stout, creeping or scandent, amply to densely scaly, the scales commonly denticulate; leaves dimorphous, commonly 1-1.5 m. long, remote, variously provided with scales and trichomes; petiole not articulate, sparsely scaly, terete abaxially, canaliculate adaxially; lamina pinnate to 3-pinnate, fertile ones greatly contracted; rachis canaliculate, with the ridges thickened; pinnae not articulate on the rachis, the costa canaliculate, the ridges thickened and continuous as a ridge along the rachis; veins commonly free, or in a few species merging to form areoles or joined at their apices by a continuous submarginal strand; fertile laminae with their divisions greatly contracted, the abaxial surface covered with sporangia (these often partially extending around to the adaxial side), indusia and paraphyses lacking; spores monolete, bilateral, with perine.

Since Fée's treatment (1845) there has been only scattered work on the genus, so the taxonomy remains rather obscure and the generic lines roughly drawn. Some workers have included within it such Asian genera as *Arthrobotrya*, *Teratophyllum*, and *Egenolfia*, although none of these is included in this treatment. (*Egenolfia* is included in *Bolbitis*, under which see further discussion.) *Polybotrya*, as circumscribed here, is essentially a free-veined, neotropical genus of 25-30 species, although it *does* include *Olfersia* (with a submarginal strand connecting the vein tips) and *Soromanes* (with a few vein branches anastomosing).

Polybotrya may be confused with another dimorphous-leafed genus, *Bolbitis*. However, species of the latter (in Guatemala) have veins copiously reticulate, ultimate soriferous segments (in ours) 0.5-2.5 cm. broad, and laminae scaly but lacking trichomes. *Polybotrya* (in Guatemala) has the fertile leaf much more constricted—0.2-0.3 (0.4) cm. broad—and the lamina is provided with both scales and trichomes; venation is generally free, although in a few species there may be some casual anastomosing of veins.

A peculiar feature not uncommon in *Polybotrya* is the occurrence of partially fertile, partially sterile leaves. On these leaves some pinnae (often the proximal ones) are no different than those of normal sterile laminae, but the apical segment of the leaf and the apices of other pinnae are greatly constricted, and a nearly continuous line of sporangia is beginning to form between the midrib and segment margin. In Guatemala, this condition has been observed in both *P. aucuparia* and *P. villosula*.

- a. Sterile lamina terminating abruptly with a conform apical "pinna"; veins approximate, commonly 1-forked at or near the base. *P. cervina*.
- a. Sterile lamina gradually tapering to a pinnatifid apex; veins subdistant, pinnately branched.
 - b. Veins anastomosing; lamina of mature sterile leaves pinnate to pinnate-pinnatifid. *P. aucuparia*.
 - b. Veins free; lamina of mature, sterile leaves 2-pinnate to 2-pinnate-pinnatifid.
 - c. Fertile lamina 3-pinnate, the ultimate (soriferous) segments ca. 1 cm. long; rhizome scales tortuous, spreading. *P. osmundacea*.
 - c. Fertile lamina 2-pinnate, or rarely 3-pinnate as to bases of lower pinnules, the ultimate (soriferous) segments 3-10 cm. long; rhizome scales firm, rigid, appressed.
 - d. Axes and (rarely) the abaxial surface short-pilose (trichomes 0.1-0.2 mm. long); costae and costules abaxially with scattered, brown, linear scales. .. *P. caudata*.
 - d. Axes and (usually) the abaxial surface long-villose (trichomes 0.5-1 mm. long); costae and costules with scales rare or lacking. *P. villosula*.

***Polybotrya aucuparia* Christ, Bull. Herb. Boissier II. 6: 166. 1906.**

In wet forests, often on slopes or along rivers or streams, sea level to 1,350 m.; Izabal; Quezaltenango; San Marcos. Southern Mexico; Honduras to Panama.

Plants terrestrial, or rooted in soil with a high-climbing rhizome; rhizome stout, to 7 mm. thick, densely provided with linear, lustrous, orange to bright-brown scales, these appressed to (more commonly) spreading, spinulose-dentate; leaves remote, to ca. 1 m. long. Sterile leaf 22-40 cm. broad; petiole 25-45 cm. long, shorter than the lamina, gray- or yellow-brown, scaly near the base; lamina pinnate to 2-pinnate, chartaceous to subcoriaceous, glabrous, tapering gradually to a pinnatifid apex; pinnae 6-12 pairs, all but the upper ones short-stalked, 10-25 cm. long and 2-6 cm. broad, spreading to ascending, lanceolate, acuminate, cuneate to obtuse (or sometimes truncate) at the often inequilateral base, commonly serrate to crenate or shallowly lobed, but occasionally on proximal ones of larger leaves cut entirely to the costa; veins subdistant, 5-12 mm. apart, pinnately branched, the branches anastomosing at acute angles with adjacent ones. Fertile leaf 12-25 cm. broad, 2-pinnate; pinnae subdistant, stalked, ascending, the ultimate (soriferous) segments 1-2 cm. long and 0.1-0.3 cm. broad.

This is a rather strange species, because of inconsistencies in the dissection of the sterile lamina. Commonly the pinnae somewhat resemble those of *P. cervina* in that they are nearly entire. Larger pinnae of more mature leaves are frequently crenate or shallowly lobed. But occasionally, as in the type collection (*Wercklé 16770*, Costa Rica), pinnae are cut nearly or quite to the costa. The simply pinnate forms scarcely differ from the South American *P. serratifolia* (Fée) Kl. or *P. polybotryoides* (Bak.) Christ, and it may even be that the three are conspecific. However, David Lellinger of U.S. National Herbarium, who has studied the genus for the Fern Flora of Southern Central America, has advised (*in litt.*) that the latter two species have

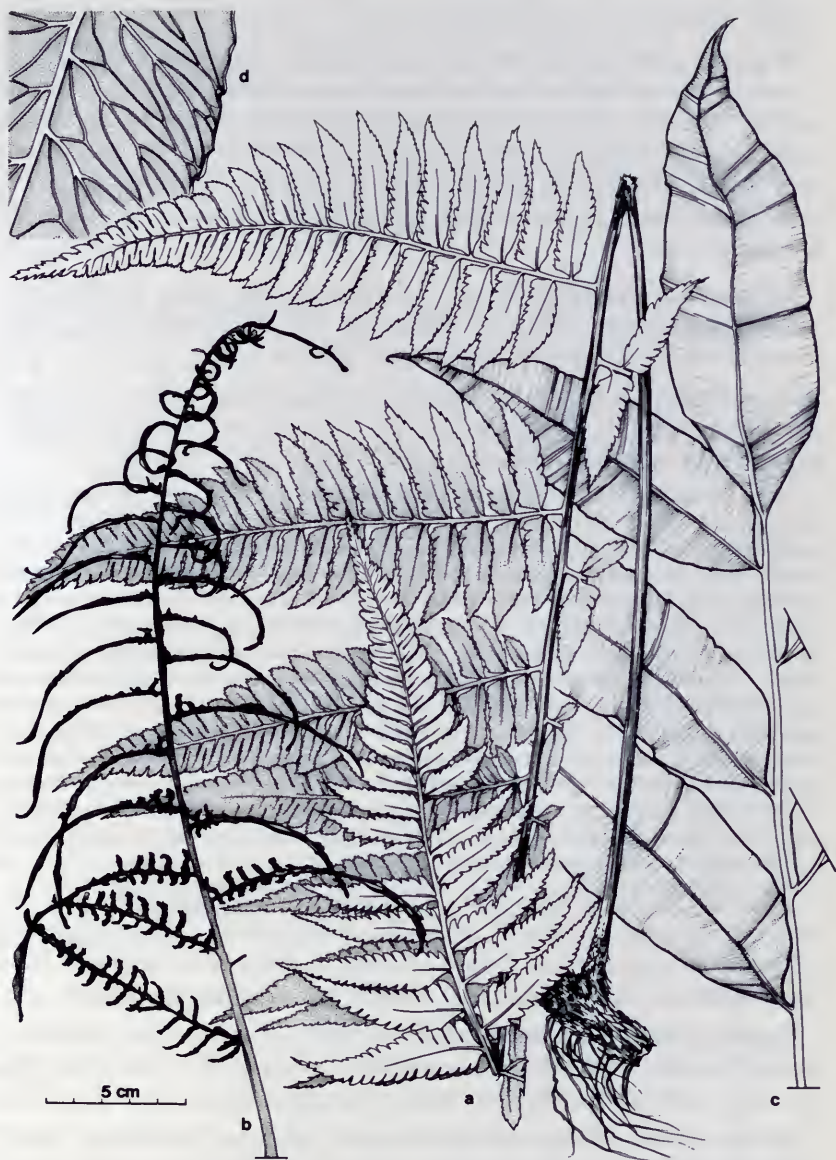


FIG. 60. *Polybotrya*. a-b. *P. villosula*: a, habit, sterile leaf, $\times \frac{1}{2}$; b, apex of fertile leaf, $\times \frac{1}{2}$; c, *P. cervina*, apex of fertile leaf, $\times \frac{1}{2}$; d, *P. aucuparia*, portion of sterile pinna, venation, $\times 1\frac{1}{2}$.

much thicker (15-20 mm.) rhizomes and are generally found at much higher (1,300-2,400 m.) altitudes.

With the paucity of specimens now available, it may be impossible to arrive at a meaningful classification of this species complex, and more careful field observations will be required throughout the range. There may be morphological differences in leaves borne on terrestrial rhizomes as opposed to those borne on climbing rhizomes, as in the case of *Maxonia* (under which see further discussion of a similar phenomenon).

Polybotrya caudata Kunze, Linnaea 9: 23. 1834. *Polypodium adiantoides* Aublet, Hist. Pl. Guianae 2: 962. 1775 (*nom. illeg.*). *Olfersia caudata* (Kunze) Kunze, *op. cit.* 21: 206. 1848.

Thus far known from one collection in Guatemala: damp rain forest, along Río Frío, alt. 65 m., Dept. Izabal, *Steyermark 39895*. Nicaragua to Colombia and the Guianas; Brazil; Peru; Bolivia; Trinidad.

Plants terrestrial, or rooted in soil with a high-climbing rhizome; rhizome stout, densely provided with firmly appressed, light-brown, linear to lanceolate scales, these subentire toward the rounded, thickened base, but erose to spinulose-dentate toward the attenuate apex; leaves distant, to 2 m. long. Sterile leaf to nearly 1 m. broad; petiole 30-70 cm. long, stramineous to light brown, scaly at base; lamina 2-pinnate to 2-pinnate-pinnatifid, gradually tapering to a pinnatifid apex, chartaceous, glabrous, or essentially so, the rachis and costae short-pilose (trichomes 0.1-0.2 mm. long); pinnae numerous, ovate or subdeltoid, spreading, stalked, acuminate, subequilateral, the costae and costules provided abaxially with scattered dark-brown, linear scales; pinnules crenate-serrate to deeply lobed, short-stalked (at least those of lower pinnae), spreading, commonly inequilateral at base (usually truncate and more strongly produced acroscopically, cuneate and somewhat reduced basiscopically); veins free, distinct, pinnate in the segments. Fertile leaf similar to sterile in size, 2-pinnate (or some larger pinnules again pinnatifid at base), the soriferous pinnules spreading, linear, to 9 cm. long and 0.3 cm. broad (except broader at the pinnatifid base).

Besides the characters used in the key there appear to be few differences between this and *P. villosula*. If this is true among specimens collected throughout the range of both species, then there is little justification in considering them more than varietally distinct.

Polybotrya cervina (L.) Kaulf. Enum. Fil. 55. 1824. *Osmunda cervina* L. Sp. Pl. 1065. 1753. *Acrostichum cervinum* (L.) Sw. Syn. Fil. 14. 1806. *Olfersia cervina* (L.) Kze. Flora 312. 1824.

In wet forests, often along swamps, sea level to 350 m.; Alta Verapaz; Izabal; Petén. British Honduras; Honduras; Costa Rica; Panama; West Indies; Colombia to Surinam, south to Bolivia and Brazil.

Plants terrestrial; rhizome stout, creeping, densely provided with linear, lustrous, orange or light-brown scales, these entire, but remotely spinulose-dentate near the

apex; leaves crowded, 0.5-1.2 m. long. Sterile leaf 25-45 cm. broad; petiole 20-50 cm. long (commonly shorter than the lamina), stramineous or light brown, scaly near the base; lamina pinnate, chartaceous to subcoriaceous, glabrous, tapering abruptly with a conform terminal "pinna"; pinnae 4-12 pairs, short-stalked, ascending, 18-28 cm. long, 3-7 cm. broad, lanceolate, long-acuminate, unequally cuneate at base, with cartilaginous, entire margins; veins approximate, slightly raised, somewhat obscure, commonly forked at or near their bases, their apices joined by a continuous, submarginal strand. Fertile leaf 15-25 cm. broad, nearly 2-pinnate; petiole 45-80 cm. long (often nearly twice the length of the lamina); pinnae subdistant, linear, strongly ascending, 8-18 cm. long, 1-3 cm. broad, the lobes subdistant, linear, joined along the costa by a narrow wing of tissue, 4-10 mm. long, 0.7-2.2 mm. broad.

Polybotrya osmundacea H. & B. in Willd. Sp. Pl. 5: 195. 1810. *P. cylindrica* Kaulf. Enum. Fil. 56. 1824. *Acrostichum osmundaceum* (H. & B.) Hook. Sp. Fil. 5: 246. 1864.

Known thus far in Guatemala from one collection: 75-225 m., on log in forest, vicinity of Quiriguá, Depto. de Izabal, *Standley 24195*. British Honduras; Costa Rica; Panama; West Indies; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Plants terrestrial, or rooted in soil with a high-climbing rhizome; rhizome stout, densely provided with spreading, linear, dull to slightly lustrous scales, these often somewhat bicolorous (brown, with paler, scarious margins), subentire or erose to denticulate; leaves subdistant, to 1.2 m. long. Sterile leaf 30-50 cm. broad; petiole 15-40 cm. long (much shorter than the lamina), stramineous to light brown, scaly at base as on the rhizome; lamina 2-pinnate-pinnatifid to nearly 3-pinnate, gradually tapering to a pinnatifid apex, chartaceous, the rachis and bases of costae hispid, the leaf surface glabrous, but commonly conspicuously orange-glandular on the abaxial side; pinnae numerous, ovate or subdeltoid, spreading, short-stalked, acuminate, subequilateral; pinnules lobed to pinnatisect, or larger ones pinnate as to the basal segments, short-stalked, spreading, inequilateral at base (truncate and strongly produced acroscopically, cuneate and somewhat reduced basiscopically), acuminate at apex, the costules often provided abaxially with scattered, dark-brown, filamentous scales; veins free, distinct, pinnate in the segments. Fertile leaf similar to the sterile in size, but 3-pinnate to 3-pinnate-pinnatifid, the ultimate (soriferous) segments spreading, linear, commonly less than 1 cm. long and 0.2 cm. broad.

Polybotrya villosula Christ, Bull. Herb. Boissier II. 6. 168. 1906.

In forests and thickets, often on slopes above streams or rivers, usually climbing tree trunks, 0-600 m.; Alta Verapaz; Izabal. British Honduras; Honduras; Nicaragua to Colombia and Ecuador.

Plants usually rooted in soil with high-climbing rhizomes; rhizome stout, densely provided with firmly appressed, light-brown, linear to lanceolate scales, these subentire toward the rounded, thickened base, but erose, denticulate, or spinulose-dentate toward the attenuate apex; leaves distant, to 1.5 m. long. Sterile leaf 30-60 cm. broad; petiole 25-50 cm. long, usually shorter than the lamina, stramineous to light brown, scaly at base; lamina commonly 2-pinnate-pinnatifid, gradually tapering to a pinnatifid apex, chartaceous, the axes and (usually) the abaxial surface long-villose (trichomes 0.5-1 mm.

long); pinnae numerous, ovate or subdeltoid, spreading, stalked, acuminate, subequilateral, the costae and costules with linear scales rare or lacking; pinnules crenate-serrate to deeply lobed, short-stalked (at least those of lower pinnae), spreading, commonly inequilateral at base (usually truncate and more strongly produced acroscopically, cuneate and somewhat reduced basiscopically); veins free, distinct, pinnate in the segments. Fertile leaf similar to sterile in size, 2-pinnate (or some larger pinnules again pinnatifid at base), the soriferous pinnules spreading, linear, to 7 cm. long and 0.2 cm. broad (except broader at the pinnatifid base).

This is very similar to *P. caudata*, under which see further discussion.

POLYPODIUM Linnaeus

REFERENCES: W. R. Maxon, A study of certain Mexican and Guatemalan species of *Polypodium*, Contr. U.S. Natl. Herb. 8: 271-276. 1903; and, *Polypodium furfuraceum* and related species, *op. cit.* 17: 557-579. 1916; and, *Polypodium squamatum* and its allies, *tom. cit.* 579-600. C. A. Weatherby, The group of *Polypodium polypodioides*, Contr. Gray Herb. 124: 22-35. 1939. A. M. Evans, Interspecific relationships in the *Polypodium pectinatum-plumula* complex, Ann. Mo. Bot. Gard. 55: 193-293. 1969. D. B. Lellinger, A revision of the fern genus *Niphidium*, Amer. Fern J. 62: 101-120. 1972.

Plants commonly epiphytic, but often epipetric or, less often, terrestrial; rhizome long- or short-creeping, rarely compact and suberect, commonly scaly, the scales clathrate or not, highly variable, from spreading and filiform to appressed and circular; leaves usually small to medium-sized, but occasionally to more than 1 m. long, monomorphic to dimorphic, typically petiolate, but sometimes sessile or subsessile; petiole nearly always articulate (commonly conspicuously so) to the rhizome or to a short phyllopodium borne on the rhizome, glabrous, pubescent, or scaly; lamina typically pinnate or pinnatifid, less commonly simple and entire (or very rarely to 3-pinnate), glabrous to pubescent, and often scaly; venation free and forked to areolate, at least some of the areoles with free, included veinlets, these excurrent or spreading in all directions; sori discrete, round to oblong or elliptic (or very rarely in a narrow, continuous or interrupted line), superficial to deeply impressed in the tissue, borne at or very near the tips of veinlets, or occasionally at the union of merging, included veinlets; indusium lacking; paraphyses lacking, or present and filiform to circular and peltate; sporangia slender-stalked, naked to glandular-papillose or setose; spores monolet, bilateral, or (rarely) globose, commonly lacking perine.

As with the delimitation of genera in Polypodiaceae, there are strongly conflicting opinions concerning the circumscription of the genus *Polypodium*. With New World species alone, various authors treat this as a single genus containing 0-12 subgenera or sections, whereas others recognize as many as a dozen separate genera. I do not feel the boundaries of these groups are clearly enough drawn to warrant generic distinction. However, insofar as the Guatemalan representatives are concerned, it has proven feasible to align the species

within a half-dozen subgenera and provided workable keys to this end. Even so, a few of the groups do not stand out as sharply as one would desire, even at the subgeneric level.

As circumscribed here, *Polypodium* is a cosmopolitan genus containing 200-225 species, the majority of which occur in tropical or subtropical regions. The following key separates the species into subgenera, after which treatments of the latter are arranged alphabetically.

- a. Leaves simple, glabrous or provided with filamentous scales, these sometimes with a broadened, peltate base (but not circular).
 - b. Sori uniseriate between costa and leaf margin; leaves dimorphous or subdimorphous (the sterile much or somewhat broader than the fertile). subg. MICROGRAMMA. p. 368
 - b. Sori 2- to many-seriate between costa and leaf margin; leaves not or scarcely dimorphous.
 - c. Sori borne in a single row between each of the primary veins; areoles very irregular in size, shape, and orientation, the free, included veinlets spreading in various directions. subg. NIPHIDIUM. p. 372
 - c. Sori borne in a double row between each of the primary veins (but single in costal areoles); areoles somewhat regular in size, shape, and orientation, the free, included veinlets always excurrent. subg. CAMPYLONEURUM. p. 359
- a. Leaves pinnatifid to decompose, or if simple then amply provided with circular, peltate scales (especially abaxially).
 - d. Venation free, or if areolate then most of the areoles bearing a single, free, excurrent veinlet; each sorus borne at or near the tip of a single veinlet. subg. POLYPODIUM p. 387
 - d. Venation areolate, many of the areoles with 1-3 free veinlets, these spreading in various directions; each sorus borne at the union of merging, included veinlets.
 - e. Lamina with scales essentially lacking; sporangia not intermixed with scales. subg. PHLEBODIUM. p. 374
 - e. Lamina amply to densely scaly; sporangia intermixed with circular-peltate scales (or in a few species such scales fugacious or lacking). subg. PLEOPELTIS. p. 377

Subgenus CAMPYLONEURUM

Rhizome long- or short-creeping, stout to thin and delicate, scaly, the scales ovate to linear-lanceolate, glabrous, commonly obviously clathrate; leaves articulate to the rhizome or very rarely (outside Guatemala) continuous, densely crowded to widely scattered, sessile to petiolate; lamina simple and subentire or very rarely (outside Guatemala) pinnate, glabrous or, rarely, minutely pubescent; venation reticulate, the primary veins joined by lateral connecting veins, forming a series of areoles between costa and leaf margin; the costal areoles with a single, free, excurrent veinlet, and the other areoles with usually 2, sometimes 3-4, free, excurrent veinlets, and often another median, percurrent veinlet dividing the primary areole into subequal pairs; sori round, superficial, 1- to many-seriate between costa and leaf margin, each sorus borne on the tip of a free veinlet within an areole; paraphyses rarely present; sporangia stalked, commonly glabrous; spores monolet, bilateral, lacking perine.

The subgenus consists of 20-25 neotropical species, fairly easily recognized by the rather consistent pattern of veins and the simple

lamina. The species, however, are often difficult to delineate, and many forms and varieties have been described on the basis of frequently nebulous characters such as leaf texture, relative prominence of veins, and degree of taper of lamina base.

- a. Rhizome long-creeping, delicate, 0.8-2 mm. thick; leaves spaced (0.8) 1-2.5 cm. apart.
 - b. Lamina 3.5-7 cm. broad, abruptly narrowed to an acute or acuminate apex and an acuminate base; primary veins mostly straight; areoles (5) 6- to 10-seriate between costa and leaf margin. *P. repens*.
 - b. Lamina 1.5-3 cm. broad, very gradually narrowed at both ends; primary veins somewhat flexuous, often gently curved; areoles 4- to 6-seriate between costa and margin. *P. serpentinum*.
- a. Rhizome short-creeping, stout, (2) 2.5-10 mm. thick; leaves crowded or approximate, 0-0.6 (1) cm. apart.
 - c. Leaves long-petiolate, petiole commonly about $\frac{1}{2}$ as long as the lamina; lamina rather abruptly narrowing, cuneate or short-decurrent at base. ... *P. tenuipes*.
 - c. Leaves short-petiolate or subsessile, petiole $\frac{1}{2}$ - $\frac{1}{10}$ (or less) the length of the lamina; lamina narrowing (commonly very gradually), and long-decurrent at base.
 - d. Primary veins conspicuous and strongly prominulous, straight or slightly flexuous; lamina (5) 6-12 cm. broad.
 - e. Petiole 5 cm. long or less (often obsolete), $\frac{1}{10}$ - $\frac{1}{20}$ (or less) the length of the lamina; lamina very gradually and regularly attenuate at base. *P. phyllitidis*.
 - e. Petiole (4-) 6-18 cm. long, $\frac{1}{5}$ - $\frac{1}{10}$ the length of the lamina; lamina cuneate to acuminate at base. *P. latum*.
 - d. Primary veins inconspicuous to obscure abaxially, or if distinct then not or only slightly prominulous, slightly to strongly flexuous; lamina 0.2-4.5 (-6) cm. broad.
 - f. Axes and leaf tissue covered (sometimes sparsely) with whitish, acicular, unicellular, minute (0.1-0.2 mm.) trichomes; lamina oblanceolate; veins (all of them) obscure. *P. occultum*.
 - f. Axes and leaf tissue glabrous; lamina linear to narrow-elliptic (rarely oblanceolate); veins evident or obscure.
 - g. Areoles in 1-3 (4) series between costa and margin; primary veins arising from the costa at a sharp (ca. 30°) angle; secondary (connecting) veins irregularly arching and joining adjacent primary veins at disproportionate levels, the areoles thus formed very irregular in shape and commonly longer than broad [*P. angustifolium*].
 - h. Leaves 0.2-1.5 (1.8) cm. broad, with petiole commonly less than 4 cm. long (often obsolete); veins obscure. .. *P. angustifolium* var. *angustifolium*.
 - h. Leaves (1.5) 2-4.2 cm. broad, the petiole commonly 4-16 cm. long; veins (at least primary ones) evident, though usually not conspicuous. *P. angustifolium* var. *amphostenon*.
 - g. Areoles in 4-8 series between costa and margin; primary veins arising from the costa at a broad (45-75°) angle; secondary (connecting) veins regularly arching and joining adjacent primary veins at nearly the same level, the areoles thus formed very regular in shape, and often nearly as broad as (or broader than) long.
 - i. Lamina rather abruptly reduced at both ends, acuminate at apex, and acuminate or acute at base; rhizome scales 1-2 mm. long, mostly broad-

lanceolate to ovate-acuminate; plants growing near sea level.

P. costatum.

- i. Lamina tapering very gradually to both ends, the apex narrowly acute to attenuate (rarely acuminate), the base gradually long-decurrent; rhizome scales mostly 3-6 mm. long, filiform (from a broader base) or linear-lanceolate; plants commonly growing at middle and upper (to 2,600 m.) elevations. *P. xalapense.*

***Polypodium angustifolium* Sw. Nov. Gen. Sp. Pl. Prodr. 130. 1788.**

Rhizome short-creeping, 3-7 mm. thick, commonly pruinose, amply to densely covered with light- to dark-brown, lustrous scales, these 2-4 mm. long, broadly ovate to lanceolate, mostly spreading, distinctly clathrate; leaves crowded or closely spaced, 0.1-0.5 cm. apart, 15-60 cm. long, 0.2-3 (4) cm. broad, sessile to short-petiolate; petiole stramineous, flattened, not or scarcely sulcate adaxially, obsolete or up to 10 cm. long, glabrous; lamina glabrous, chartaceous to coriaceous, opaque, dull, or slightly lustrous adaxially, linear to narrow-elliptic, the margins slightly cartilaginous, slightly to strongly revolute, the apex subacute to narrowly acute or attenuate, the base gradually attenuate; veins obscure to indistinct, not prominulous, primary ones arising from the costa at a sharp (30° or less) angle, rather flexuous; secondary (connecting) veins sharply and irregularly arching and joining adjacent primary veins at disproportionate levels, the areoles thus formed very irregular in shape and commonly much longer than broad; areoles in 1-3 (4) series between costa and margin, the costal areoles with a single, excurrent, free veinlet and the other areoles with 1-2 excurrent veinlets, these slightly dilated at the tips and there sometimes provided with small, circular, cretaceous dots adaxially; sori borne on the tips of free veinlets.

Several varieties have been recognized, but the lines between these are mostly arbitrary and nearly impossible to define. The principal "difference" has been that of breadth of lamina, ranging from 0.2-0.3 cm. in var. *ensifolium* to about 3 cm. in var. *amphostenon*. This has been coupled with features which are a natural result of the broadening of lamina, such as a greater number of areoles (and thus more numerous sori) between costa and margin. For purposes of this treatment I recognize only the typical, and var. *amphostenon*. As indicated in the key, the broadening of lamina can at least be coupled with evident (*vs.* completely obscure) veins.

***Polypodium angustifolium* var. *amphostenon* (Kze. ex Kl.) Bak.** in Mart. Fl. Brasil 1 (2): 530. 1870 (not Hieron. 1905). *P. amphostenon* Kze. ex Kl. Linnaea 20: 399. 1847. *Campyloneuron amphostenon* (Kze. ex Kl.) Fée [as "amphostemon"], Mém. Fam. Foug. 5 (Gen. Fil.): 258. 1852. *C. angustifolium* var. *amphostenon* (Kze. ex Kl.) Farw. Amer. Mid. Naturalist 12: 296. 1931.

In forests and wooded ravines, on tree trunks and stumps, occasionally on mossy rocks or on clay banks, 1,700-3,400 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; El Pro-

greso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Totonicapán. Hispaniola; southern Mexico; Honduras; El Salvador to Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Leaves 32-85 cm. long, (1.5) 2-4.2 cm. broad, with petiole (3) 4-16 cm. long; lamina narrow-elliptic, the margins plane to slightly revolute; primary veins evident abaxially, though commonly indistinct, not or scarcely prominulous; areoles commonly in 2-3 series between costa and leaf margin.

Polypodium angustifolium var. **angustifolium**. *P. ensifolium* Willd. in L. Sp. Pl. 5: 182. 1810. *Cyrtophlebium angustifolium* (Sw.) J. Sm. Bot. Mag. (Compend.) 72: 12. 1846. *Campyloneuron angustifolium* (Sw.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 257. 1852. *Goniophlebium angustifolium* (Sw.) Brack. in Wilkes, Explor. Exped. 16: 33. 1854. *C. ensifolium* (Willd.) J. Sm. Cat. Cult. Ferns 12. 1857. *P. angustifolium* var. *gramineum* Sod. Crypt. Vasc. Quit. 366. 1893. *P. angustifolium* var. *ensifolium* (Willd.) Hicken, Rev. Mus. La Plata 15: 271. 1908. *C. angustifolium* var. *ensifolium* (Willd.) Farw. Amer. Mid. Naturalist 12: 296. 1931. *Calaguuala*.

In and at edges of forests, in wooded ravines or (occasionally) in clearings, commonly on trunks and branches of trees, but also on rocks or clay banks, sea level to 3,100 m.; very common, and thus far reported from all departamentos except Chiquimula and Jutiapa. Florida; West Indies; Mexico; Central and South America.

Leaves 15-60 cm. long, 0.2-1.5 (1.8) cm. broad, the petiole obsolete or short (commonly less than 4 cm.); lamina linear to narrow-elliptic, the margins slightly to strongly revolute; veins obscure; areoles commonly in 1-2 series between costa and leaf margin.

Cooking the leaves of this fern and drinking the decoction before meals is reputed to be a remedy for throat infection and asthma (*vide* Steyermark, Huehuetenango).

Polypodium costatum Kze. Linnaea 9: 38. 1834 (not Mett. 1857 nor Hook. 1863). *Campyloneurum costatum* (Kze.) Presl, Tent. Pterid. 190. 1836. *Cyrtophlebium costatum* (Kze.) J. Sm. J. Bot. (London) 1: 196. 1842. *Campyloneurum phyllitidis* var. *costatum* (Kze.) Farw. Amer. Mid. Naturalist 12: 297. 1931.

Rare, in forests or wooded ravines, near sea level, Petén. Greater Antilles; Trinidad; southern Mexico; British Honduras; Honduras; El Salvador; Nicaragua; Panama; Colombia; Ecuador.

Rhizome short-creeping, 2.5-5 mm. thick, sparsely provided with tawny to dark-brown, dull or sublustrous scales, these 1-2 mm. long, broadly lanceolate to ovate-acuminate; leaves densely crowded or closely spaced, 0.1-0.5 cm. apart, 20-55 cm. long, 2.5-5 (5.5) cm. broad, petiolate; petiole stramineous to light brown, flattened or subterete, shallow-sulcate adaxially, glabrous, 2.5-12 cm. long; lamina glabrous, chartaceous to subcoriaceous, opaque, dull, or slightly lustrous adaxially, oblanceolate, or

narrow-elliptic or -oblong, the margins cartilaginous, plane, or slightly revolute, the apex commonly long-acuminate, the base acute or (typically) acuminate (*i.e.*, rather abruptly narrowing and then long-decurrent along the petiole); veins distinct to obscure, not prominulous, primary ones arising from the costa at a broad (45-75°) angle, flexuous; secondary (connecting) veins regularly and gently arching and joining adjacent primary veins at about the same level, the areoles thus formed regular in shape, and often nearly as broad as, or broader than, long; areoles in 5-8 series between costa and margin, the costal areoles with a single, free, excurrent veinlet, the other areoles with 2 free, excurrent veinlets, or sometimes with a third, median veinlet which divides the areoles into subequal pairs; sori borne on the tips of free veinlets.

This and *P. xalapense* are very similar, the latter perhaps deserving only varietal status. The lamina in *P. costatum* typically narrows very abruptly to an acuminate apex, and usually equally so at base, whereas that of *P. xalapense* narrows gradually and nearly imperceptibly to both ends (or rarely the apex acuminate). Leaf texture of *P. costatum* is commonly coarse (chartaceous to subcoriaceous), while that of *P. xalapense* is typically firm-herbaceous (rarely thicker). Free, excurrent veinlets in the latter often bear small, cretaceous dots on their tips adaxially, whereas such dots are rarely, if ever, present on *P. costatum*. *Polypodium costatum* is not uncommon in the Greater Antilles, but is very rare in Guatemala. *Polypodium xalapense* apparently is not found outside of Central America, where it is quite common, especially in southern Mexico and Guatemala.

***Polypodium latum* (Moore) Moore ex Sodiro, Crypt. Vasc. Quitensis. 371. 1893. *Campyloneurum latum* Moore, Index Fil. 225. 1861. *P. phyllitidis* var. *β latum* (Moore) Hook. Sp. Fil. 38. 1863. *P. phyllitidis* forma *latum* (Moore) Proctor, Bull. Inst. Jamaica Sci. Ser. 5: 49. 1953.**

In or at the edges of forests, often along streams or rivers, on tree trunks or branches or rotting logs, sometimes on mossy rocks or on wet soil, sea level to 1,200 m.; Alta Verapaz; Izabal; Retalhuleu. Florida; West Indies; southern Mexico; British Honduras; Honduras to Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Rhizome short-creeping, 5-12 mm. thick, often completely covered by masses of brown-tomentose roots and sparsely provided with broadly ovate, brown, dull or sublustrous, clathrate scales, these mostly appressed, to 5 mm. long; leaves densely crowded, 40-130 cm. long, 5-12 cm. broad, petiolate; petiole stramineous or light brown, rounded abaxially, flattened to sulcate adaxially, (4) 6-18 cm. long ($\frac{1}{3}$ - $\frac{1}{10}$ the length of the lamina), glabrous, but sparsely scaly near the base; lamina chartaceous to subcoriaceous, essentially glabrous, dull to slightly lustrous (especially adaxially), broadly ligulate, narrow-elliptic, the margins cartilaginous and commonly undulate, the apex acute to acuminate, the base short- to long-cuneate, or acuminate (*i.e.*, rather abruptly narrowing and then decurrent along the petiole); primary veins conspicuous and strongly prominulous, essentially straight; secondary (connecting) veins commonly evident (distinct or indistinct), arching gently to form a series of 8-18 areoles between costa and

margin, some (especially distal) areoles divided into pairs by a median, excurrent veinlet which is essentially parallel to primary veins, or sometimes divided into 3-4 secondary areoles by 2-3 excurrent, free veinlets, 1 each in the costal areoles and 2 (sometimes 3-4) each in the others.

It is with great reluctance that I maintain this as a distinct species, for it is surely nothing more than a variety of *P. phyllitidis*, as recognized by Hooker (1863), or a form of the latter (Proctor, 1953). The major distinction appears to be the nearly obsolete petiole, coupled with a more gradually tapering lamina base, as in *P. phyllitidis*, as opposed to a distinctly petiolate, more abruptly tapering lamina in *P. latum*. But these features are not always consistent, and even less so are other characteristics described by various authors, such as greater number of sori between main veins, plane *vs.* undulate leaf margins, relative size and number of secondary areoles, etc. The relationship needs closer scrutiny, including an examination of specimens throughout the very broad range of distribution.

Polypodium occultum Christ, Bull. Herb. Boissier II. 5: 7. 1905. *Campyloneurum occultum* (Christ) Meyer ex Lehl. Proc. Biol. Soc. Wash. 89: 709. 1977.

In forests, on tree trunks, not yet reported from Guatemala, but to be expected here. Occurring at 100-1,000 m.; British Honduras; Honduras; Nicaragua; Costa Rica; Panama.

Rhizome short-creeping (2) 2.5-3 mm. thick, sparsely provided with dark-brown, dull or somewhat lustrous scales, these filiform to lanceolate from a broad base, mostly spreading, 1-3 mm. long; leaves crowded, 0.1-0.3 cm. apart, 10-32 (35) cm. long, 1.5-4.5 cm. broad, sessile to short-petiolate; petiole stramineous, rounded or flattened abaxially, sulcate adaxially, obsolete or up to 3 cm. long, this and the costa sparsely to amply provided with minute (0.1-0.2 mm.), acicular, whitish, unicellular trichomes; lamina firm-herbaceous to chartaceous, opaque, dull, or sublustrous adaxially, oblanceolate, the margins scarcely cartilaginous, plane to slightly repand or undulate, the apex acute to acuminate, the base gradually and regularly attenuate, the surface (at least abaxially) amply but minutely hispidulous as on the axis; veins obscure, at least abaxially, primary ones somewhat flexuous, secondary (connecting) veins arching rather strongly to form a series of 3-5 areoles between costa and margin, the costal areoles with a single, excurrent, free veinlet, and the other areoles with usually 2 excurrent veinlets; sori borne on tips of free veinlets, and bearing numerous tawny or orange, filamentous paraphyses (abortive sporangia?).

Polypodium phyllitidis L. Sp. Pl. 1083. 1753. *Campyloneurum phyllitidis* (L.) Presl, Tent. Pterid. 190. 1836. *Cyrtophlebium phyllitidis* (L.) J. Sm. J. Bot. (London) 4: 58. 1841.

In forests or wooded ravines, on trunks of trees, sea level to 1,500 m.; Alta Verapaz; Izabal; Petén; Quezaltenango; Suchitepéquez. Florida; West Indies; Mexico to Panama; South America.

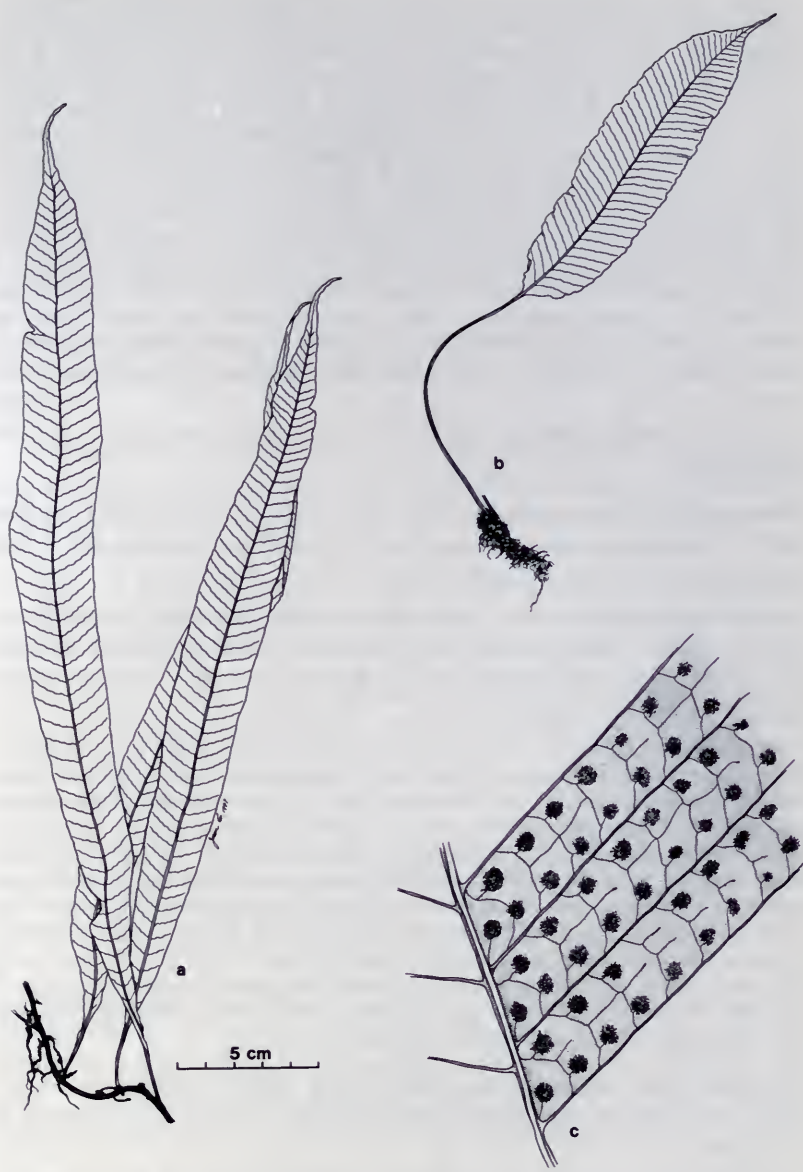


FIG. 61. *Polypodium* subgenus *Campyloneurum*. a, *P. serpentinum*, habit, $\times \frac{1}{2}$; b, *P. tenuipes*, habit, $\times \frac{1}{4}$; c, *P. phyllitidis*, portion of lamina, venation, $\times 3$.

Rhizome short-creeping, 5-10 mm. thick, often completely covered by masses of brown-tomentose roots and sparsely provided with broadly ovate, brown, sublustrous, clathrate scales, these mostly appressed, to 5 mm. long; leaves densely crowded, 35-100 cm. long, (5) 6-10 cm. broad, subsessile or very short-petiolate; petiole stramineous or light brown, rounded abaxially, flattened to sulcate adaxially, glabrous, 5 cm. long or less, $\frac{1}{10}$ - $\frac{1}{20}$ the length of the lamina; lamina chartaceous, essentially glabrous, somewhat lustrous (especially adaxially), ligulate, narrow-elliptic or oblanceolate, the margins cartilaginous, essentially plane, but often slightly undulate or irregularly repand, the apex rounded to acute or, rarely, short-acuminate, the base gradually and rather regularly attenuate; primary veins conspicuous and strongly prominulous, essentially straight; secondary (connecting) veins evident, distinct or indistinct, arching gently to form a series of 7-16 areoles between costa and margin, some (especially distal) areoles divided into pairs by a median, excurrent veinlet which is parallel to primary veins (or sometimes divided into 3-4 secondary areoles by 2-3 excurrent veinlets); sori borne on tips of excurrent, free veinlets, 1 each in the costal areoles and 2 (rarely 3) each in the others.

This is scarcely distinct from *P. latum*, under which see further discussion.

Polypodium repens Aubl. Hist. Pl. Guian. 2: 962. 1775 (not Sw. 1788). *Campyloneurum repens* (Aubl.) Presl, Tent. Pterid. 190. 1836. *Cyrtophlebium repens* (Aubl.) J. Sm. J. Bot. (London) 4: 58. 1841.

Climbing on tree trunks in forests or wooded ravines, 20-1,000 m.; Alta Verapaz; Izabal; Petén; Sololá. West Indies; southern Mexico; British Honduras; Honduras to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Rhizome long-creeping, 1-2 mm. thick, sparsely to amply provided with dull-brown, ovate to lanceolate scales, these 1-3 mm. long, mostly appressed, clathrate; leaves usually well-spaced, 0.8-2 cm. apart, 25-40 cm. long, 3.5-7 cm. broad, short-petiolate; petiole stramineous, rounded abaxially, flattened to sulcate adaxially, alate for most of its length by the tissue of the decurrent lamina, free portion 0.5-2 (3) cm. long; lamina firm-herbaceous, subglabrous, dull, or slightly lustrous adaxially, narrow-elliptic to oblanceolate, the apex acute or acuminate, the base typically acuminate (i.e., rather abruptly narrowing and then long-decurrent along the petiole almost to the rhizome); primary veins conspicuous, prominulous, and straight (and usually stramineous) nearly to the leaf margin; secondary (connecting) veins arching broadly to form a series of (5) 6-10 areoles between costa and margin; sori borne on the tips of excurrent, free veinlets, 1 each in costal areoles, and 2 each in the others.

Polypodium serpentinum Christ, Bull. Herb. Boissier II. 6: 51. 1906. *Campyloneurum serpentinum* (Christ) Ching, Sunyatsenia 5: 263. 1940.

Climbing on tree trunks in forests or wooded ravines, 900-1,700 m.; apparently not yet reported from Guatemala, but to be expected here, as it has been found in southern Mexico (Chiapas) and from Honduras to Panama, Colombia and Peru.

Rhizome long-creeping, delicate, 0.8-2 mm. thick, sparsely provided with scattered, dull-brown, linear or linear-lanceolate scales, these 1-2 mm. long, mostly appressed, subclathrate; leaves rather well-spaced, 1-2.5 cm. apart, 20-34 cm. long, 1.5-3 cm. broad, short-petiolate; petiole stramineous, rounded abaxially, flattened or sulcate adaxially, alate for most of its length by the tissue of the decurrent lamina, free portion 0.6-2 cm. long, lamina thin- to firm-herbaceous, glabrous, not or scarcely lustrous, narrow-elliptic, narrowed equally and very gradually at both ends, at the apex to a narrowly acute to subcaudate tip (this often broken off in dried specimens), and at base very long-decurrent almost to the rhizome; primary veins somewhat prominulous and conspicuous, commonly rather sinuous and often gently curved near the margin; secondary veins arching broadly to form a series of 4-6 areoles between costa and margin; sori borne on the tips of excurrent, free veinlets, 1 each in costal areoles, and 2 each in the others.

***Polypodium tenuipes* (Maxon) C. Chr. Index Fil. Suppl. 63. 1913. *Campyloneurum tenuipes* Maxon, Contr. U.S. Natl. Herb. 13: 7. 1909.**

In forests or wooded ravines, often along streams or rivers, on tree trunks, mossy rocks, or wet banks, 1,200-2,600 m.; Alta Verapaz (type from near Cobán, on rocks in forest, alt. 1,350 m., *Tuerckheim II-1952*); Quezaltenango; San Marcos; Sololá. Mexico (Chiapas).

Rhizome short-creeping, (3) 4-8 mm. thick, amply to densely provided with dull-brown, linear or lanceolate, attenuate scales, these 3-7 mm. long, appressed to spreading, clathrate; leaves crowded to approximate, 0.1-1 cm. apart, mature ones 40-90 cm. long, 5-8 cm. broad, long-petiolate; petiole stramineous or light brown, rounded abaxially, flattened to sulcate adaxially, glabrous, but with a few scales at base, 15-35 cm. long, commonly about $\frac{1}{2}$ as long as the lamina; lamina chartaceous, glabrous, dull, or slightly lustrous adaxially, narrow-elliptic or oblanceolate, the margins cartilaginous and slightly repand or undulate, the apex abruptly long-acuminate, the base acute, narrowly to broadly cuneate or (rarely) short-decurrent; primary veins commonly rather conspicuous and somewhat prominulous, essentially straight; secondary (connecting) veins usually indistinct, arching gently or sharply to form a series of 6-9 areoles between costa and margin, some (especially distal) areoles divided into pairs by a median, excurrent veinlet which is parallel to the primary veins; sori borne on tips of excurrent, free veinlets, 1 each in the costal areoles, and commonly 2 each in the others.

***Polypodium xalapense* (Fée) Christ, Bull. Soc. Roy. Bot. Belgique 35: 231. 1896. *Campyloneurum xalapense* Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 258. 1850-52. ? *C. caudatum* Fée, *op. cit.* VIII: 96. 1857 (not *P. caudatum* Raddi, 1819 nor Mett. 1857). *P. weatherbyanum* Seymour, Phytologia 31: 171. 1975 (*nom. nov.* based on *C. caudatum* Fée).**

In forests or wooded ravines, on trunks of trees, or rarely on rocks or clay banks, 500-2,600 m.; Alta Verapaz; Chimaltenango; Escuintla; Guatemala; Jalapa; Quezaltenango; Sacatepéquez; San Marcos; Santa

Rosa; Sololá; Suchitepéquez. Southern Mexico; British Honduras; Honduras; El Salvador to Panama.

Rhizome short-creeping, 2.5-8 mm. thick, amply provided with light- or dark-brown, sublustrous scales, most of these 3-6 mm. long, linear-lanceolate to filiform (from a broader base); leaves densely crowded or closely spaced, 0.1-0.6 cm. apart, 25-75 cm. long, 2-5 (5.5) cm. broad, short-petiolate; petiole stramineous to light brown, flattened or subterete, sulcate adaxially, glabrous, 2-6 (10) cm. long; lamina glabrous, firm-herbaceous to chartaceous (rarely subcoriaceous), dull, or scarcely lustrous adaxially; narrow-elliptic, tapering very gradually from at or near the middle to both ends, the apex very narrowly acute to attenuate (very rarely acuminate), the base gradually long-decurrent, the margins cartilaginous, plane or slightly revolute, commonly somewhat undulate; veins evident, but often the secondary ones indistinct, not or scarcely prominulous, primary ones arising from the costa at a broad (50-60°) angle, slightly flexuous; secondary (connecting) veins regularly and gently arching and joining adjacent primary veins at about the same level, the areoles thus formed regular in shape and often nearly as long as (or broader than) long; areoles in 4-7 series between costa and margin, the costal areoles with a single, free, excurrent veinlet (this often tipped with a cretaceous dot adaxially), the other areoles with 2 free, excurrent veinlets and commonly with a third, median veinlet dividing the areoles into subequal pairs; sori borne on tips of free veinlets.

A number of collections from southern Mexico and Guatemala have been observed in various herbaria, determined as "*Campyloneuron caudatum* Fée," and these are nothing more than *P. xalapense*. Although I have not seen the specimen designated as the type (*Schaffner 176*, from "Cordoba et Huatusco, Mexique") Fée's description easily fits *P. xalapense*. Such collections at Gray Herbarium have been annotated by Weatherby as "new name apparently necessary," since the name *Polypodium caudatum* was used earlier for other ferns by various authors. Thus Seymour (1975) was prompted to designate *P. weatherbyanum* as a *nom. nov.*, based on *C. caudatum* Fée.

With this species possibly might be included *P. costatum*, which does not differ significantly. See treatment of the latter for further discussion.

Subgenus MICROGRAMMA

Plants epiphytic; rhizome creeping, scaly, the scales commonly narrow to filiform from a broader, peltate base, not or scarcely clathrate; leaves dimorphous or subdimorphous (the sterile much or somewhat broader than the fertile), widely spaced, sessile or short-petiolate, articulate to the rhizome or to short phyllopodia arising from the rhizome; lamina simple and entire, glabrous, or provided with filamentous scales (these sometimes with a broadened, peltate base, but never circular); venation areolate, of 2 kinds, the veins either forming a single row of costal areoles, each of these containing a single free, excurrent veinlet, or abundantly reticulate with areoles each containing 1 to several veinlets spreading in all directions; sori borne within the areoles, in a single line between costa and leaf margin; paraphyses few to numerous, usually filiform or consisting of very narrow scales; sporangia naked; spores monolete, 2-lateral, usually reniform.

Microgramma is a rather weakly defined subgenus, recognized primarily by its simple, usually glabrous and dimorphous leaves. There are about 20 species, all neotropical, and two or three others in Africa.

- a. Veins commonly forming a single row of costal areoles, each containing a single, free, excurrent veinlet; rhizome 0.4-0.8 (1) mm. thick (including scales); lamina amply but minutely scaly.
- b. Fertile lamina 1.5-2.5 mm. broad, with mature sori projecting beyond the margin; adaxial laminar scales castaneous (occasionally tawny); plants growing at 50-300 m.
P. ciliatum.
- b. Fertile lamina 3-9 mm. broad, sori not projecting beyond the margin; adaxial laminar scales whitish (occasionally tawny); plants growing at 1,000-1,350 m.
P. piloselloides.
- a. Veins abundantly reticulate, areoles with 1 to several included veinlets spreading in all directions; rhizome 1-7 mm. thick (including scales); lamina glabrous or essentially so.
- c. Rhizome 1-3 mm. thick, the scales tawny to castaneous; sterile lamina 1-2 cm. broad; fertile lamina 0.6-1 cm. broad; primary veins much more prominent than secondary ones. *P. lycopodioides*.
- c. Rhizome 3-7 mm. thick, the scales tawny to whitish; sterile lamina (2) 2.5-4 cm. broad; fertile lamina (1) 1.2-3 cm. broad; primary and secondary veins equally prominent. *P. palmeri*.

Polypodium ciliatum Willd. in L. Sp. Pl. 5: 144. 1810 (not Spr. 1821 nor Boj. 1837). *Acrostichum reptans* Cav. Anales Hist. Nat. 1: 104. 1799 (not *P. reptans* Gmel. 1791). *Goniophlebium ciliatum* (Willd.) J. Sm. in Hook. Gen. Fil. t. 51. 1840. *Craspedaria ciliata* (Willd.) Link, Fil. Sp. 117. 1841. *Microgramma ciliata* (Willd.) Alston, Bull. Jard. Bot. Etat. 27: 56. 1957. *M. reptans* (Cav.) A. R. Sm. Proc. Calif. Acad. Sci. 40: 230. 1975.

In forests, on trunks or branches of trees, 50-300 m; Alta Verapaz; Izabal. Southern Mexico; British Honduras; Honduras; Nicaragua; Costa Rica; Panama; Trinidad & Tobago; Colombia to the Guianas, south to Bolivia and Brazil.

Rhizome long-creeping, 0.4-0.8 mm. thick, amply scaly, the scales appressed to somewhat spreading, 2-3 mm. long, linear-attenuate to filiform, castaneous to tawny, nonclathrate, the margins sometimes minutely and remotely denticulate; leaves chartaceous, opaque, numerous, widely spaced, subsessile to short-petiolate, strongly dimorphous; sterile lamina (1.2) 1.5-5 cm. long, 0.8-1.5 cm. broad, acute or subacute, ovate, elliptic, oblanceolate or oblong, provided on both surfaces, margins and midrib with minute scales, these castaneous, appressed, filiform to lanceolate-attenuate from a peltate base; venation goniophleboid, a single row of costal areoles, each with a single, free, included, excurrent veinlet, the other vein branches essentially free; fertile lamina like the sterile but very constricted, (2) 3-6 cm. long, 0.15-0.25 cm. broad; sori borne in the costal areoles, forming a single line on each side of the midrib, large and crowded and at maturity projecting beyond the leaf margin; paraphyses numerous, conspicuous, consisting of castaneous, filamentous scales.



FIG. 62. *Polypodium* subgenus *Microgramma*. a, *P. ciliatum*, habit, fertile and sterile leaves, $\times \frac{1}{2}$; b, *P. piloselloides*, portion of lamina showing venation; c-d, *P. palmeri*: c, habit, fertile and sterile leaves, $\times \frac{1}{2}$; d, portion of lamina showing venation.

This is very similar to *P. piloselloides*, and perhaps should be included with it as a variety as did Hooker and Baker (Syn. Fil. p. 340, 1867). In Central America the altitudinal and the few morphological differences (as used in the key) are rather consistent. But in South America these features begin to merge and become less significant.

Polypodium lycopodioides L. Sp. Pl. 1082, 1753 (not Schkur. 1809). *P. salicifolium* Willd. in L. Sp. Pl. 5: 149. 1810 (not Hook. 1862). *Pleopeltis lycopodioides* (L.) Presl, Tent. Pterid. 193. 1836. *Phlebodium lycopodioides* (L.) J. Sm. Curtis Bot. Mag. 72: Compend. 12. 1846. *Phymatodes prominula* Maxon, Contr. U.S. Natl. Herb. 10: 501. 1908. *Polypodium prominulum* (Maxon) C. Chr. Index Fil. Suppl. 61. 1913. *Microgramma lycopodioides* (L.) Copel. Gen. Fil. 185. 1947.

In wet forests, on trunks and branches of trees, sea level to 800 m.; Alta Verapaz; Izabal. West Indies; southern Mexico (Chiapas) to Panama; Colombia to the Guianas, south to Brazil and Bolivia; Old World tropics.

Rhizome long-creeping, 1-3 mm. thick (including scales), completely covered with scales, these appressed, but the tips commonly spreading, 3-5 mm. long, ovate to lanceolate, peltately attached near the base, hair-tipped, not or scarcely clathrate, the margins subentire to slightly erose or minutely and remotely denticulate, castaneous to tawny, usually darkest at base; leaves chartaceous, opaque, numerous, widely spaced, sessile or short- (to 3 mm.) petiolate, subdimorphous; sterile lamina 3-8 cm. long, 1-2 cm. broad, acute or subacute, lanceolate or narrow-elliptic, glabrous or essentially so, margins slightly cartilaginous and plane to slightly revolute; venation amply reticulate, except at the leaf margin, primary veins prominulous or not, much more conspicuous than the secondary ones, areoles irregular, many of them containing 1-several free veinlets, these spreading in all directions; fertile lamina like the sterile, but commonly narrower, (2.5) 4-8 cm. long, 0.6-1 cm. broad; sori large, round, commonly impressed in the tissue, borne in the principal (paracostal) areoles, forming a single line medial between midrib and each leaf margin; paraphyses sometimes extending beyond the sporangia, but typically filiform, few, and inconspicuous.

Polypodium palmeri Maxon, Contr. U.S. Natl. Herb. 17: 600. 1916. *Phlebodium nitidum* J. Sm. Curtis Bot. Mag. 72: Compend. 13. 1846 (not *Polypodium nitidum* Klf. 1824). *Microgramma nitida* (J. Sm.) A. R. Sm. Proc. Calif. Acad. Sci. 40: 230. 1975.

In forests, on trunks and branches of trees, sea level to 200 m.; Izabal; Petén. Mexico; British Honduras; Honduras; Nicaragua; Panama.

Rhizome long-creeping, 3-7 mm. thick (including scales), completely covered with scales, these appressed, 4-7 mm. long, ovate to lanceolate, peltately attached near the base, attenuate to hair-tipped, not or scarcely clathrate, subentire, tawny to whitish, but often ferruginous along the center or at the base; leaves firm-herbaceous to charta-

ceous, numerous, widely spaced, subsessile or short- (to 1 cm.) petiolate, subdimorphous; sterile lamina 6-15 cm. long, (2) 2.5-4 cm. broad, obtuse (rarely subacute), typically broad- or narrow-oblong, occasionally elliptic or lanceolate, glabrous or essentially so, margins slightly cartilaginous and plane to slightly revolute; venation abundantly reticulate (except free at the tips), primary veins not or scarcely more prominent than the secondary ones, areoles irregular, many of them containing 1 to several free veinlets, these spreading in all directions; fertile lamina like the sterile, but typically narrower and acute or subacute, 8-16 cm. long, (1) 1.2-3 cm. broad; sori large, round, not or scarcely impressed, borne in the principal (paracostal) areoles, forming a single line medial between midrib and each leaf margin; paraphyses commonly numerous, filiform, or often conspicuous and consisting of brown, filamentous scales.

Polypodium piloselloides L. Sp. Pl. 1083. 1753. *Marginaria piloselloides* (L.) Presl, Tent. Pterid. 187. 1836. *Goniophlebium piloselloides* (L.) J. Sm. in Hook. Gen. Fil. t. 51. 1840. *Craspedaria piloselloides* (L.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 264. 1852. *Lepicystis piloselloides* (L.) Diels in Engl. & Prantl Pflanzenf. 1(4): 323. 1899. *Microgramma piloselloides* (L.) Copel. Gen. Fil. 185. 1947.

In forests, on trunks or branches of trees, 1,000-1,350 m.; Alta Verapaz (apparently represented in Central America by only a few Guatemalan collections). West Indies; Colombia; Venezuela; British Guiana; Brazil; Ecuador; Peru; Bolivia.

Rhizome long-creeping, 0.4-1 mm. thick, amply scaly, the scales appressed to somewhat spreading, 2.5-4 mm. long, lanceolate-attenuate to filiform, castaneous to tawny, nonclathrate, the margins sometimes minutely and remotely denticulate; leaves chartaceous, opaque, numerous, widely spaced, subsessile or short- (to 2 cm.) petiolate, somewhat to strongly dimorphous; sterile lamina 1.5-5 (7) cm. long, 0.6-1.5 cm. broad, obtuse or subacute (in ours) to acute, ovate to elliptic to oblanceolate, provided on both surfaces, margins and midrib with minute scales, these appressed, filiform to lanceolate-attenuate from a frequently broadened, peltate base, those on the abaxial side tawny to mostly orange or castaneous, on the adaxial side tawny to mostly whitish; venation goniophleboid, a single row of costal areoles, each with a single free, included, excurrent veinlet, the other vein branches essentially free; fertile lamina like the sterile but relatively much narrower, 2-6 (7) cm. long, 0.3-0.9 cm. broad; sori large, borne in the costal areoles, forming a single line on each side of the midrib, rarely reaching and never projecting beyond the leaf margin; paraphyses numerous, conspicuous, consisting of castaneous, filamentous scales.

With this perhaps should be included *P. ciliatum*, under which see further discussion.

Subgenus NIPHIDIUM

Plants epiphytic, sometimes epipetric or terrestrial; rhizome short- to long-creeping, with roots usually densely tomentose, scaly, the scales ovate to lanceolate, mostly clathrate, concolorous or bicolorous (with a dark-colored central portion and lighter colored margins); leaves few, approximate, subsessile or short-petiolate, articulate to the rhizome or to short (ca. 5 mm.) phyllopodia arising from the rhizome; lamina simple,

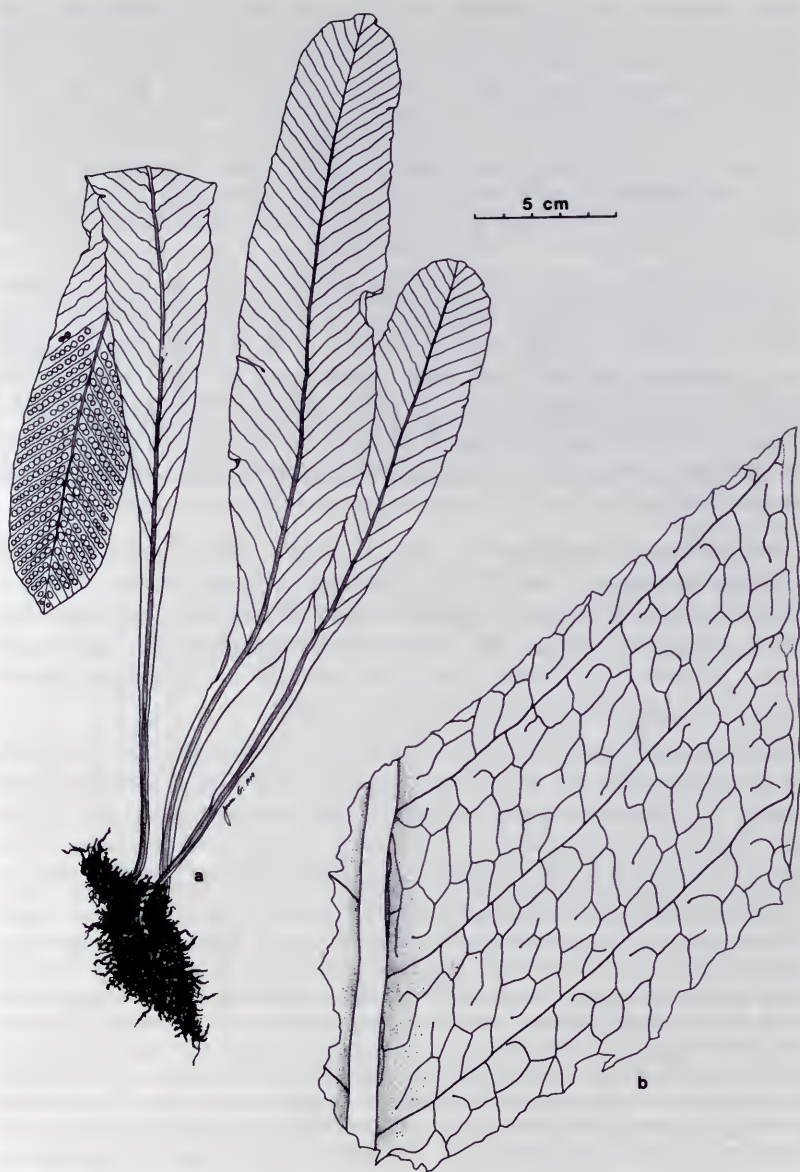


FIG. 63. *Polypodium* subgenus *Niphidium*. a-b, *P. crassifolium*: a, habit, $\times \frac{1}{2}$; b, detail of venation, $\times 3$.

entire, coriaceous, essentially glabrous (as in ours), or scaly on the abaxial side, often glaucous, oblanceolate, elliptic-lanceolate, or ligulate, usually long-attenuate at base; primary veins commonly prominulous and conspicuous, strongly ascending, straight, joined by numerous, immersed, and inconspicuous secondary veins, these forming irregular areoles containing included free veinlets which may be oriented in any direction, the tips of which often terminate in hydathodes which are visible from the adaxial side; sori large, round (rarely somewhat elongated), borne in single rows between the primary veins, commonly 4- to 12-seriate between midrib and lamina margin; paraphyses (abortive sporangia) sparse to numerous; sporangia naked or (as in ours) ciliate; spores monolet, bilateral, smooth, probably without perine.

In his revision of *Niphidium* (as a genus), Lellinger (1972) recognized 10 species, all neotropical. Most of the species are nearly impossible to separate except for the character of rhizome scales, these being distinguished by their color (bicolorous *vs.* concolorous), the configuration of the margin, or the shape of cells. Most species have a rather restricted range, primarily in small areas of South America, but the only species found in Guatemala also occurs generally throughout the neotropics.

Polypodium crassifolium L. Sp. Pl. 2: 1083. 1753. *Anaxetum crassifolium* (L.) Schott, Gen. Pl. 1. 1834 (*nom. illeg.*) *Phymatodes crassifolia* (L.) Presl, Tent. Pterid. 197. 1836. *Pleopeltis crassifolia* (L.) Moore, Index Fil. lxxviii. 1857. *Pessopteris crassifolia* (L.) Underw. & Maxon, Contr. U.S. Natl. Herb. 10: 485. 1908. *Niphidium crassifolium* (L.) Lell. Amer. Fern J. 62: 106. 1972.

In forests and wooded ravines, on trunks or larger branches of trees, sea level to 1,600 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Huehuetenango; Izabal; Petén; Quezaltenango; El Quiché; San Marcos; Suchitepéquez; occasionally found in other areas cultivated as a garden plant. West Indies, Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Plants epiphytic, rarely terrestrial or epipetric; rhizome short-creeping, the scales 0.5-1 cm. long, ovate to lanceolate, acuminate, commonly bicolorous, gray-brown to blackish, with tan margins; leaves 40-125 cm. long, 2.5-12 cm. broad, short-petiolate; petiole 1-15 cm. long, yellowish brown, terete at base, otherwise flattened, commonly sulcate adaxially; lamina narrowly oblanceolate (rarely lanceolate or ligulate), obtuse to acute at apex, long-attenuate at base, the margins entire, cartilaginous, and commonly revolute, glabrous (but sometimes a few scales scattered along the midrib abaxially); primary veins prominulous, ascending (ca. 45°), straight and conspicuous all the way to the lamina margin; sori large, round, 6- to 10-seriate between midrib and lamina margin; sporangia ciliate (but the minute trichomes often deciduous at maturity).

Subgenus PHLEBODIUM

Plants epiphytic, or occasionally terrestrial; rhizome creeping, stout, densely scaly, the scales narrow, short-ciliate; leaves large, widely scattered along and articulate to the

rhizome, petiolate; lamina deeply pinnatisect, essentially glabrous, sometimes glaucous; segments elongated, subentire or obscurely crenate, joined to each other by a broad, usually rounded sinus; venation essentially reticulate, the primary veins connected near the base by a transverse veinlet, thus forming a costal areole, and otherwise separated by numerous areoles, many of these with excurrent, included veinlets which commonly merge at their tips (but some areoles, especially toward the segment margin, without included veinlets); sori round (occasionally elongated), superficial, 1- to 7-seriate between costa and segment margin, each sorus borne within an areole at the union of merging, included veinlets; paraphyses lacking; sporangia stalked, glabrous; spores monolete, oblong, usually tuberculate, lacking perine.

This is a small, neotropical subgenus consisting of two to six species, depending upon the degree of importance one is willing to assign varietal characters.

- a. Sori 1- (2-) seriate between costa and segment margin; lamina with segments 2-3 (4) cm. broad; primary veins irregularly flexuous, no more prominent than the secondary ones and their branches. *P. aureum*.
- a. Sori (2) 3-7 seriate between costa and segment margin; lamina with segments 3-7 cm. broad; primary veins straight and commonly more prominent than the secondary ones. *P. decumanum*.

***Polypodium aureum* L. Sp. Pl. 1087. 1753. *P. leucatomos* Poir. in Lam. Encycl. 5: 516. 1804. *P. areolatum* H. & B. ex Willd. in Sp. Pl. 5: 172. 1810. *Phlebodium aureum* (L.) J. Sm. J. Bot. (London) 4: 59. 1841. *Calaguala*.**

In open forests, on tree trunks, or occasionally in soil or on mossy rocks, 1,200-2,200 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; Suchitupéquez; Zacapa. Florida; West Indies; Mexico to Bolivia and Brazil.

Plants epiphytic or, occasionally, terrestrial; rhizome creeping, densely scaly, to 2 cm. thick (including scales), the scales orange to ferruginous, thin, commonly translucent, linear or linear-lanceolate, attenuate, 1-2 cm. long, the margins short-ciliate; leaves few, widely scattered along the rhizome, 30-120 cm. long, 18-50 cm. broad, petiolate; petiole 10-40 cm. long, $\frac{1}{2}$ as long as to nearly equaling the lamina, 2-5 mm. thick, smooth and glabrous, stramineous to dark brown, terete abaxially, canaliculate adaxially; lamina chartaceous, glabrous, occasionally glaucous abaxially, deeply pinnatisect, broadly oblong to subdeltoid, with a subconform apical segment, not or scarcely reduced at base; segments 6-18 pairs, spreading or slightly ascending, adjacent ones joined by a broadly rounded sinus, 10-20 cm. long, 2-3 (4) cm. broad, ligulate and obtuse to lanceolate and acute, the margins cartilaginous, broadly and obscurely crenate; primary veins oblique and irregularly flexuous, no more prominent than the secondary ones, adjacent ones connected near the base by a transverse veinlet (thus forming a narrow, costal areole), otherwise irregularly branched and anastomosing, the areoles often with included veinlet(s), the latter free or merging with each other at the tips; sori round (or occasionally elongated), in 1 (or irregularly 2) series between costa and margin, each sorus borne within an areole at the tips of merging, included veinlets (or occasionally at the tip of a single veinlet).

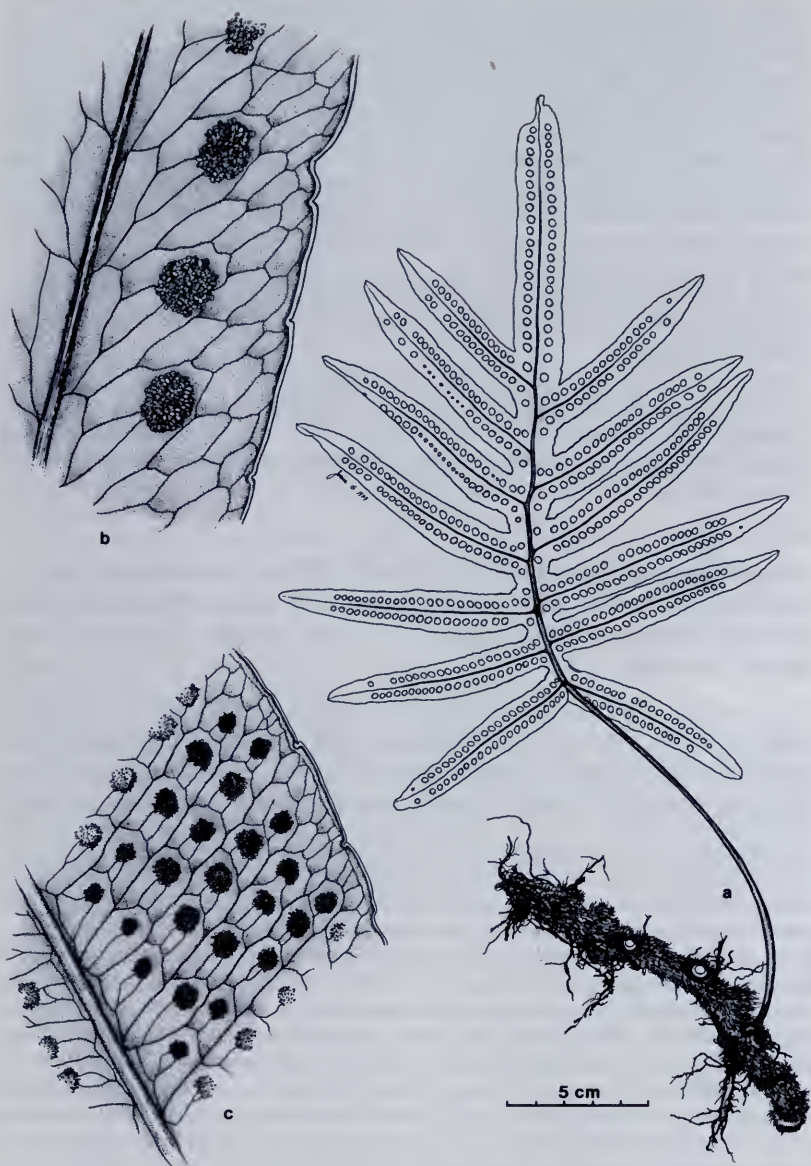


FIG. 64. *Polypodium* subgenus *Phlebodium*. a-b, *P. aureum*: a, habit, $\times \frac{1}{2}$; b, portion of lamina showing sori and venation, $\times 6$; c, *P. decumanum*, portion of lamina showing sori and venation.

Some authors recognize slight variants of the species: var. *areolatum* (H. & B. ex Willd.) Bak. throughout the entire range, and var. *araneosum* (M & G.) Brause, from Mexico. The first supposedly has narrower pinnae, always glaucous beneath. The second is a form which has small, dark, filiform, ciliolate scales scattered over the abaxial surface of the segments. A few authors even recognize this as a distinct species, although in all other characters it is no different from the typical.

Polypodium aureum has been variously described in Guatemala as having medicinal value, usually as a decoction prepared with the rhizome. Thus used, it is reputed to be a remedy for coughs and for kidney ailments.

Polypodium decumanum Willd. in L. Sp. Pl. 5: 170. 1810. *Phlebodium decumanum* (Willd.) J. Sm. J. Bot. (London) 4: 59. 1841. *P. multiseriale* Moore & Houlst. Gard. Chron. 1855: 469. 1855.

In forests, or more often in pastures, meadows, or clearings, on tree trunks (mostly palms), sea level to 500 m.; Alta Verapaz; Baja Verapaz; Izabal; Petén; Santa Rosa. West Indies; Mexico; British Honduras; Honduras; Colombia to the Guianas, south to Argentina and Paraguay.

Plants epiphytic; rhizome creeping, densely scaly, to 2 cm. thick (including scales), the scales orange, thin, and nearly transparent, linear or linear-lanceolate, attenuate, 1-2 cm. long, the margins closely short-ciliate; leaves few, widely scattered along the rhizome, 40-160 cm. long, 20-80 cm. broad, petiolate; petiole 12-55 cm. long, $\frac{1}{2}$ as long as to nearly equaling the lamina, 2-8 mm. thick, smooth and glabrous, terete, and yellow-brown to castaneous abaxially, broadly and shallowly canaliculate and commonly lighter in color adaxially, lamina glabrous, firm-herbaceous to chartaceous, deeply pinnatisect (or sometimes fully pinnate at base), broadly oblong, with a subconform apical segment, not or scarcely reduced at base; segments 4-10 pairs, ascending, or basal ones spreading, adjacent ones joined by a broadly rounded sinus, 10-40 cm. long, 3-7 cm. broad, acute to acuminate, the margins conspicuously cartilaginous, broadly (and very shallowly) crenate; primary veins straight, parallel, and prominent nearly to the segment margin, adjacent ones connected near the base by a transverse veinlet (thus forming a narrow, costal areole), and each pair separated by a double row of subequal areoles running out to the segment margin, each areole with 2-3 included, subparallel veinlets, most of which are joined at their apices; sori round, (2) 3- to 7-seriate between costa and margin, each sorus borne within an areole at the tips of merging, included veinlets.

Subgenus PLEOPELTIS

Plants commonly epiphytic; rhizome long-creeping, scaly, the scales broad or circular and peltate to narrow and spreading, not or slightly clathrate; leaves small to medium-sized, articulate to the rhizome, approximate to widely spaced, monomorphic or subdimorphic, long- or short-petiolate; lamina simple and entire to pinnatifid or occa-

sionally pinnate, amply to densely scaly, the scales commonly peltate, circular to ovate-acuminate or -attenuate; venation areolate, many (or at least a few) of the areoles with 1-3 free, included veinlets which spread in various directions; sori borne at the union of merging, included veinlets, superficial or impressed in the tissue, discrete, orbicular to ovoid or ellipsoid (or, in *P. bradeorum*, linear, continuous or interrupted), the sporangia commonly intermixed with circular-peltate scales, or in a few species such scales fugacious or lacking; spores monolete, bilateral, lacking perine.

This is one of the more distinctive subgenera of *Polypodium*, notable for its generally small leaves, abundant, circular-peltate scales, and phlebodioid venation, *i.e.*, the areoles containing free veinlets which spread in all directions, and the sori borne at the union of merging, included veinlets. The subgenus is pantropical and contains about 30-40 species.

- a. Sori linear, continuous or interrupted; leaves either simple or pinnatifid.
P. bradeorum.
- a. Sori orbicular, ovoid or ellipsoid; leaves *always* simple, or *always* pinnatifid (but never both conditions in 1 species).
- b. Leaves pinnatifid (rarely pinnate).
- c. Leaf segments linear or linear-lanceolate, typically 10-20 times as long as broad; rhizome scales strongly bicolorous, lustrous black with brown margins.
P. angustum.
- c. Leaf segments oblong, elliptic or broadly lanceolate, typically 3-7 times as long as broad; rhizome scales essentially concolorous, ferruginous to orange (sometimes with slightly paler margins).
- d. Rhizome commonly pruinose, the scales with entire or slightly erose margins; leaf segments obtuse (rarely acute), abaxially provided with orange to castaneous, essentially concolorous scales. *P. munchii*.
- d. Rhizome not pruinose, the scales with conspicuously erose-ciliolate margins; leaf segments acute, abaxially provided with bicolorous scales, these orange to castaneous, with whitish or tawny margins. *P. pleolepis*.
- b. Leaves simple, unlobed.
- e. Rhizome scales circular, 0.3-0.4 mm. in diameter, blackish, usually completely obscured by a dense covering of trichomes; sori elongated, commonly 2-4 times as long as broad. *P. astrolepis*.
- e. Rhizome scales ovate or lanceolate, 0.7-3 mm. long, not obscured by trichomes (some minute, circular, blackish scales underlying the larger ones in *P. percussum*); sori orbicular to ovoid, 1-1.5 times as long as broad.
- f. Sporangia surrounded by dense masses of filiform, ferruginous to castaneous paraphyses; plants of low elevations (sea level to 800 m.). . . *P. percussum*.
- f. Sporangia intermixed with few to many circular-peltate scales, these usually fugacious; plants of middle and high elevations (900-4,000 m.).
- g. Rhizome scales subentire to minutely erose-denticulate; lamina typically narrow-oblongate (rarely lanceolate); elevation (2,400) 2,600-4,000 m. [*P. peltatum*].
- h. Laminar scales (abaxially) approximate to imbricate, often obscuring the tissue, the circular, peltate ones commonly 0.4-1 mm. in diameter.
P. peltatum var. *peltatum*.
- h. Laminar scales (abaxially) scattered, never crowded, the circular, peltate ones commonly 0.2-0.3 mm. in diameter. . *P. peltatum* var. *interjectum*.

- g. Rhizome scales conspicuously erose-denticulate to -ciliate; lamina lanceolate or linear-lanceolate; elevation 900-2,400 (2,800) m. [*P. lanceolatum*].
- i. Rhizome scales intermixed, and often beset at their bases, with ferruginous trichomes, nonclathrate, with lumina not or scarcely evident; laminar scales subentire to denticulate. . . . *P. lanceolatum* var. *trichophorum*.
- i. Rhizome scales without trichomes, subclathrate, with most lumina small but evident; laminar scales erose-ciliate or -fimbriate.
- j. Lamina chartaceous, at least some of the veins darkened and slightly prominulous and thus somewhat evident; rhizome scales both bicolorous and pale and concolorous. . . . *P. lanceolatum* var. *crassinervatum*.
- j. Lamina coriaceous, the veins obscure; rhizome scales bicolorous, commonly tawny, with lustrous blackish centers.
P. lanceolatum var. *lanceolatum*.

Polypodium angustum (H. & B. ex Willd.) Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 186 (seors. 34). 1849. *Pleopeltis angusta* H. & B. ex Willd. Sp. Pl. 5: 211. 1810. *Phlebodium angustum* (H. & B. ex Willd.) J. Sm. J. Bot. (London) 4: 59. 1841. *Calaguala*.

In forests, thickets, wooded ravines, or occasionally in clearings, on trees, mossy rocks, or rarely on moist clay banks, 900-2,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Zacapa. Mexico; Honduras; El Salvador; Nicaragua; Brazil; Paraguay.

Rhizome long-creeping, 1.5-2.5 mm. thick, densely scaly, the scales 0.5-1 mm. long, ovate or lanceolate, bicolorous, lustrous black, with erose to erose-denticulate or -ciliate, brown margins, nonclathrate, these intermixed, and often beset at base, with filiform, tortuous, ferruginous trichomes; leaves monomorphic, petiolate; petiole 2-12 cm. long, yellowish, reddish or grayish brown, often narrow-marginate for much of its length; lamina firm-herbaceous to subcoriaceous, deeply pinnatifid, 5-15 cm. long and often as broad, broadest at the decurrent base, terminating in a subconform apical segment which is as long as or longer than the lateral ones, sparsely scaly adaxially and amply so abaxially, the scales widely scattered, of 2 kinds, ovate-acuminate and circular-peltate, 0.1-0.4 mm. broad, bicolorous, blackish, castaneous or light brown, with the paler margins erose or erose-lacerate; lamina segments 1-3 pairs, linear or linear-lanceolate, acute, joined by broadly rounded sinuses, the margins cartilaginous, entire or broadly and obscurely crenulate, plane or somewhat revolute; veins obscure, phlebotoid, rather abundantly areolate, a few of the areoles with 1-2 free, included veinlets which are variously directed; sori superficial to slightly immersed, borne in 2 lines on a segment, 1 on either side of the costa, usually ovoid, often so large as to project over the segment margin, the sporangia intermixed with few to many blackish, bicolorous, circular, peltate scales which are very early deciduous or shriveling.

This is very closely related to *P. lanceolatum*, being very similar in characters such as rhizome and lamina scales, venation, texture, and sori. It differs significantly only in its deeply pinnatifid lamina.

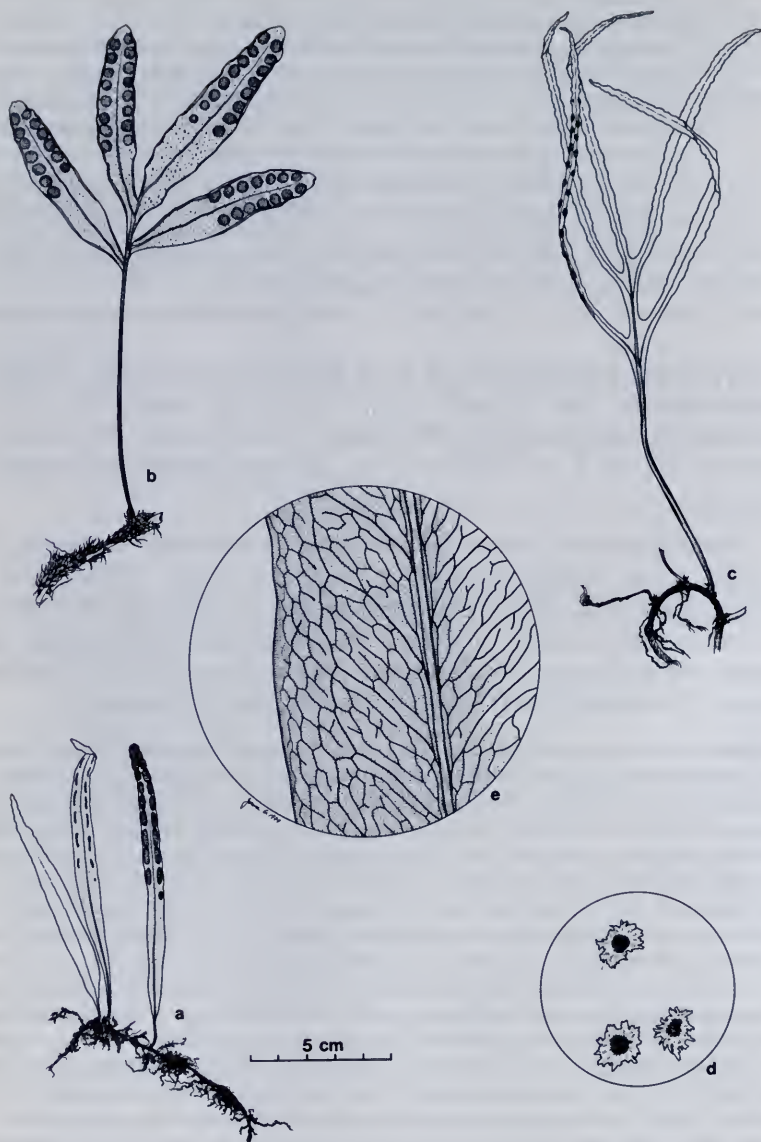


FIG. 65. *Polypodium* subgenus *Pleopeltis*. a, *P. astrolepis*, habit, $\times \frac{1}{2}$; b, *P. munchii*, habit, $\times \frac{1}{2}$; c, *P. angustum*, habit, $\times \frac{1}{2}$; d, *P. lanceolatum* var. *crassinervatum*, rhizome scale, $\times 25$; e, *P. percussum*, venation, $\times 6$.

Polypodium astrolepis Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 185 (seors. 33). 1849. *Grammitis lanceolata* Schkuhr, Krypt. Gewächse. 1: 9, t. 7. 1806 (not *Polypodium lanceolatum* L. 1753). *G. elongata* Sw. Syn. Fil. 22 & 213. 1806. *G. revoluta* Spreng. ex Willd. in L. Sp. Pl. 5: 139. 1810 (not *P. revolutum* C. Chr. 1906). *P. elongatum* (Sw.) Mett. Abh. Senckenberg Naturf. Ges. 2: 88. 1857 (not Aiton, 1789). *Gymnogramma elongata* (Sw.) Hook. Sp. Fil. 5: 157. 1864. *Pleopeltis astrolepis* (Liebm.) Fourn. Mex. Pl. 1: 87. 1872. *Phlebodium astrolepis* (Liebm.) Conz. Fl. Taxon. Mex. 1: 100. 1939. *Pleopeltis revoluta* (Spreng. ex Willd.) A. R. Sm. Proc. Calif. Acad. Sci. 40: 230. 1975.

In forests and wooded ravines, occasionally in clearings, on trunks and branches of trees, on logs, or rarely on mossy rocks, 30-1,800 m.; Alta Verapaz; Escuintla; Guatemala; Huehuetenango; Izabal; Petén; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Suchitepéquez. West Indies; Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Rhizome long-creeping, 0.5-1 mm. thick, amply provided with minute (0.3-0.4 mm.), blackish, circular, peltate scales, these appressed, not or scarcely clathrate, usually completely obscured by a dense covering of castaneous trichomes; leaves chartaceous to coriaceous, opaque, approximate to widely spaced, subsessile or short- (to 8 mm.) petiole, essentially monomorphic; petiole strongly flattened, usually marginate or alate to base, sparsely provided with minute, appressed, circular scales; lamina simple, entire, 5-17 cm. long, 0.3-1.8 cm. broad, obtuse to (commonly) acute, linear-lanceolate to narrow-elliptic or oblanceolate, costa lighter in color than, or concolorous with, the leaf tissue adaxially, castaneous or blackish abaxially, both laminar surfaces minutely scaly, the scales widely scattered, lacerate-stellate, the rays whitish from a castaneous or blackish base; veins fine, immersed (but commonly visible when held to light), copiously anastomosing, a few of the areoles containing free veinlets, these variously directed; sori large, oblong or elliptic, commonly 2-4 times as long as broad, superficial or somewhat impressed, commonly confined to the distal half (or third) of the lamina, a few peltate scales intermixed with the sporangia, but these soon withering or deciduous and thus rarely seen.

Polypodium bradeorum Rosenst. Repert. Spec. Nov. Regni Veg. 10: 279. 1912. *P. colysoides* Max. & Copel. Univ. Calif. Publ. Bot. 19: 292. 1941.

Thus far not reported from Guatemala, but to be expected here, for it is known to occur in southern Mexico and in British Honduras. On trees, in undisturbed forests or in cacao or banana plantations, sea level to 600 (-1,300) m.; southern Mexico; British Honduras; Nicaragua; Costa Rica.

Rhizome long-creeping, 2-3 mm. thick, abundantly scaly, the scales 2-4 mm. long, lanceolate or linear-lanceolate, often attenuate, ferruginous to orange, the margins mi-

nutely and irregularly erose or erose-denticulate and sometimes lighter in color, sub-clathrate (the lumina small but evident under slight magnification); leaves essentially monomorphic, petiolate; petiole 5-20 cm. long, shorter or longer than the lamina, amply scaly, yellowish brown, rounded to flattened abaxially, sulcate adaxially, conspicuously alate especially in the distal portion; lamina simple and lanceolate or elliptic to 3-lobate or pinnatisect, long- and narrow-decurrent, firm-herbaceous and somewhat translucent, 8-16 cm. long, naked or sparsely scaly adaxially, amply scaly abaxially, the scales widely scattered, of 2 kinds, lanceolate- to ovate-acuminate, and circular-peltate, 0.1-0.3 mm. broad, faintly bicolorous, orange to ferruginous, the margins pale to whitish and conspicuously erose-lacerate to -ciliate; segments (on pinnatifid leaves) 1-3 pairs, lanceolate to elliptic, joined by a broadly rounded sinus, the margins plane, not or scarcely cartilaginous, entire or obscurely crenate or crenulate; veins evident, somewhat phlebooid, irregularly areolate, some of the areoles with 1-2 free, included veinlets which are variously directed (or on some plants free veinlets lacking); sori superficial, linear, continuous or interrupted, oblique, borne on the primary veins and often extending from costa nearly to the segment margin, peltate scales rare or lacking among the sporangia.

This curious fern has been placed by various authors in two different species, and even in its own genus. Based on the original collections, some simple-leaved plants from Costa Rica were determined as *P. bradeorum*, and pinnatifid ones from Mexico as *P. colysoides*. Gómez (Brenesia 10/11: 116. 1977) has decided it is sufficiently distinct (primarily because of the linear sori and some peculiarities of venation) to be placed in a new genus, *Pseudocolysis*. Since the species was first named, much discussion has been published concerning its relationship with the Old World genus, *Colysis* Presl, and the subgenera of *Polypodium*: *Microgramma* and *Pleopeltis*. With the present lack of agreement by pteridologists on the circumscription of many of the genera or subgenera within *Polypodium sens. lat.*, I am hesitant at this time to recognize *P. bradeorum* as yet another genus, and am not even sure of its place in either of the weakly defined subgenera, *Microgramma* or *Pleopeltis*. However, for the present, I prefer to follow Evans and Mickel (Brittonia 21: 255-260. 1969) in placing these heteromorphic plants under *P. bradeorum* and, for purposes of this Flora, tentatively assigning the species to subgenus *Pleopeltis*. (For a comprehensive discussion of the problem see Evans & Mickel, *loc. cit.*)

***Polypodium lanceolatum* L. Sp. Pl. 1082. 1753.**

Rhizome long-creeping, branched, 0.8-2.5 mm. thick, densely covered with ovate to lanceolate, often acuminate scales, these 0.7-2 mm. long, with margins erose-denticulate to -ciliate, subclathrate, with lumina somewhat distinct, or nonclathrate (in var. *trichophorum*); leaves 6-32 cm. long, 0.5-2.5 cm. broad, monomorphic to subdimorphic (sterile ones sometimes slightly broader), short-petiolate; petiole terete (at least in ours), narrow-marginate for most or all of its length; lamina lanceolate or linear-lanceolate, chartaceous to coriaceous, subacute to short-acuminate, the margins somewhat cartilaginous, often revolute, the surfaces scaly, the scales widely scattered, usu-

ally of 2 kinds, most of them peltate, circular, 0.1-0.5 mm. in diameter, castaneous to ferruginous, with a whitish to tawny margin, these intermixed with a few to many, larger, lanceolate- to ovate-acuminate ones; veins phlebotoid, obscure or indistinct, rather abundantly areolate, some of the areoles with 1 or 2 free, included veinlets which are variously directed; sori often somewhat immersed, large, 1-5 mm. long, orbicular to ovoid, the sporangia intermixed with few to many circular, peltate scales, these blackish in the center, with orange or tawny, erose margins, commonly fugacious.

With this perhaps should be included *P. peltatum*. In Weatherby's treatment of the group (1922) he distinguished the two species merely by some very subtle scale characters: those of *P. lanceolatum* erose-serrulate, with median lumina of rhizome scales more or less evident; those of *P. peltatum* (as *P. polylepis*) entire to denticulate, with lumina of rhizome scales not evident. Moreover, in this same treatment, Weatherby described the new var. *trichophorum*, differing from typical *P. lanceolatum* in that its rhizome scales often bear brownish trichomes and that their lumina are not or scarcely evident. The latter character thus linked his new variety with *P. peltatum*, and this bond is further strengthened by the fact that specimens of *P. peltatum*, especially var. *interjectum*, are often seen to have brownish trichomes on and intermixed with rhizome scales.

With many more collections now available, it would appear that the group of *P. lanceolatum* needs further examination, in order to reassess specific and varietal relationships.

Polypodium lanceolatum* var. *crassinervatum (Fée) Weath. Contr. Gray Herb. 65: 8. 1922. *Drynaria crassinervata* Fée, Mém. Fam. Foug. 8: 97. 1857. *Pleopeltis crassinervata* (Fée) Moore, Index Fil. 345. 1862. *Polypodium crassinervatum* (Fée) Kiaersk. Catal. Fil. Herb. Hort. Bot. Haun. 49. 1874.

In forests, on trees, and (rarely) on shaded, mossy rocks, 900-1,500 m.; Alta Verapaz. Southern Mexico; Honduras; Nicaragua.

Rhizome scales 1-2 mm. long, the margins erose-denticulate to ciliate, tawny to orange or frequently with blackish centers (those at petiole bases and growing tips typically longer and concolorous), subclathrate, most of the lumina narrow-rectangular and distinct; leaves 10-20 cm. long, 0.6-1.8 (2) cm. broad, essentially monomorphic (occasionally sterile ones slightly broader); petiole 1-4 (6) cm. long, terete; lamina commonly linear-lanceolate, acute or short-acuminate, chartaceous, subtranslucent, with the costa commonly blackish abaxially, scaly, the scales of the abaxial surface widely scattered, circular, 0.2-0.4 mm. in diameter, with an erose-ciliate or -fimbriate margin, and intermixed with some larger, ovate-acuminate ones; veins often obscure, but at least some of them darkened or slightly prominulous and thus somewhat evident; sori medial, rarely supramedial on broader laminae.

***Polypodium lanceolatum* var. *lanceolatum*.** *P. macrocarpum* Bory ex Willd. in L. Sp. Pl. 5: 147. 1810 (not Presl, 1825). *Grammitis*

lanceolata (L.) Schkuhr, Krypt. Gewächse 1: 9. 1806 (not Sw. 1801). *Pleopeltis lanceolata* (L.) Klf. Enum. Fil. 245. 1824. *P. macrocarpa* (L.) Klf. loc. cit. *Phlebodium lanceolatum* (L.) J. Sm. J. Bot. (London) 4: 59. 1841. *Marginaria lanceolata* (L.) Herter, Rev. Sudamer. Bot. 6: 131. 1940.

Thus far not reported from Guatemala, but to be expected here, as it is known to occur in southern Mexico, Nicaragua, and Jamaica. It is a species with wide distribution, growing on trees or stumps, occasionally on rocks, usually at altitudes of 1,200-2,000 m., in the Greater Antilles, Mexico, Nicaragua to Panama, most of South America and in the Old World tropics.

Rhizome scales 1-2 mm. long, the margins erose-ciliate or -ciliate, tawny to orange, commonly with blackish centers, subclathrate, most of the lumina distinct and isodiametric to narrow rectangular; leaves 6-20 (24) cm. long, 0.5-1.8 (2) cm. broad, essentially monomorphic; petiole 0.5-3 (5) cm. long, terete; lamina commonly linear-lanceolate, acute, coriaceous, opaque, with the costa yellowish, brown or blackish abaxially, scaly, the scales of the abaxial surface widely scattered, circular, 0.2-0.5 mm. in diameter, with an erose-ciliate or -fimbriate margin, and intermixed with many, larger ovate-acuminate ones; veins obscure; sori medial, rarely supramedial on broader laminae.

Polypodium lanceolatum* var. *trichophorum Weath. Contr. Gray Herb. 65: 8. 1922. *Phlebodium lanceolatum* var. *trichophorum* (Weath.) Conz. Fl. Taxon. Mex. 1 (2): 101. 1939. *Pleopeltis macrocarpa* var. *trichophora* (Weath.) Pic. Serm. Webbia 23 (1): 189. 1968.

In forests (rarely in clearings), on trunks of trees, or sometimes on mossy rocks, 1,350-2,400 (2,800) m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Zacapa. Mexico; Honduras; El Salvador; Nicaragua.

Rhizome scales 0.7-1 (1.5) mm. long, lanceolate or narrow-ovate, often acuminate, erose-denticulate to -ciliate, lustrous black with tawny, orange, or tan margins (those at petiole bases 2-3 mm. long and often concolorous), intermixed and often beset at their bases, with tortuous, filiform, ferruginous trichomes, cell walls thickened, lumina minute, rarely evident; leaves 6-32 cm. long, 0.5-2.5 (3) cm. broad; subdimorphic, sterile ones often somewhat broader; petiole 1-6 cm. long, terete; lamina lanceolate or linear-lanceolate, acute or subacute, coriaceous, opaque, with the costa commonly blackish abaxially, scaly, scales of the abaxial surface widely scattered, circular, 0.1-0.3 mm. in diameter, with a subentire to minutely denticulate margin, and intermixed with a few, larger, ovate-acuminate ones; veins obscure, or rarely faintly evident abaxially; sori medial, or supramedial on broader laminae.

Polypodium munchii Christ, Bull. Herb. Boissier II. 3: 147. 1903. *Pleopeltis munchii* (Christ) A. R. Sm. Proc. Calif. Acad. Sci. 40: 230. 1975.

In forests and wooded ravines, on trees, 2,200-3,300 m.; Sololá; Toninicapán. Southern Mexico; Honduras; El Salvador.

Rhizome long-creeping, commonly pruinose, 1.8-4 mm. thick, abundantly scaly, the scales 2.5-5 mm. long, ovate to lanceolate, acute or acuminate, ferruginous to orange, concolorous, with entire or slightly erose margins, nonclathrate; leaves monomorphous, long-petiolate; petiole 4-12 cm. long, commonly as long as the lamina, light brown to atropurpureous, abaxially terete, adaxially shallow-sulcate, obscurely marginate or ribbed toward the apex; lamina 3-lobate to deeply pinnatisect or pinnate, coriaceous, 4-10 cm. long and often as broad, broadest at the often decurrent base, terminating in a conform apical segment, naked adaxially, abaxially scaly, the scales widely scattered, of 2 kinds, ovate-acuminate, and circular-peltate, 0.1-0.5 mm. broad, essentially concolorous, orange to castaneous, the margins entire to faintly erose; lamina segments (or pinnae) 1 or 2 (3) pairs, oblong, elliptic or oblanceolate, acute to (most commonly) obtuse, 4-7 cm. long, 0.8-1.7 cm. broad, typically 3-5 times as long as broad, sessile or subsessile, or when adnate, joined by narrow, acute sinuses, the margins commonly revolute, entire; veins obscure (usually even when held to light), phleboid, rather abundantly areolate, some of the areoles with 1-2 free, included veinlets which are variously directed; sori superficial, borne in a single line on each side of the costa, orbicular, large, often filling the area between costa and margin, but never projecting beyond the margin, the sporangia intermixed with few to many orange to castaneous, circular, peltate scales which are very early deciduous or shriveling.

***Polypodium peltatum* Cav. Descr. Pl. 244. 1802.**

Rhizome long-creeping, often branched, 1-2 mm. thick, densely covered with ovate or broadly lanceolate scales, these 1.5-3 mm. long, with margins subentire or minutely erose (rarely remote-denticulate), not clathrate, with lamina minute and scarcely evident, these sometimes intermixed, and beset at their bases, with filiform, ferruginous trichomes; leaves 6-30 cm. long, 0.5-2.5 cm. broad, monomorphous to subdimorphous (sterile ones sometimes slightly broader), petiolate; petiole terete, narrow-marginate for some or most of its length; lamina typically narrow-oblanceolate, occasionally linear-lanceolate, chartaceous to coriaceous, acute, the margins entire to weakly repand, somewhat cartilaginous, plane, or occasionally revolute, the surfaces scaly, often copiously so abaxially, the scales of 2 kinds, most of them peltate, circular, 0.3-1 mm. in diameter, castaneous to ferruginous, with a whitish to tawny, entire to slightly erose or erose-denticulate margin, these intermixed with larger, lanceolate to ovate-acuminate ones; veins obscure or indistinct (even when held to light), phleboid, rather abundantly areolate, some of the areoles with 1 or 2 free, included veinlets, which are variously directed; sori often immersed, large, 1-5 mm. long, orbicular to ovoid, the sporangia intermixed with few to many circular, peltate scales, these blackish in the center, with orange or tawny, erose margins, commonly fugacious.

Polypodium peltatum is difficult to distinguish from *P. lanceolatum*, and the two perhaps should be considered only varietally distinct (see treatment of the latter for further discussion). Two varieties of *P. peltatum* have been recognized, the typical, which is rare in Guatemala, and var. *interjectum*, which is rather frequent at higher elevations.

Polypodium peltatum var. **interjectum** Weath. Amer. Fern J. 34: 17. 1944. *Pleopeltis macrocarpa* (Bory ex Willd.) Klf. var. *interjecta* (Weath.) A. R. Smith, Amer. Fern J. 70: 26. 1980.

In forests, occasionally in clearings or meadows, on trunks and branches of trees, rarely on rocks, (2,400) 2,600-4,000 m.; Chimaltenango (type from Cerro de Tecpám, 2,400-2,700 m., *Standley 60957*); Guatemala; Huehuetenango; Quezaltenango; San Marcos; Sololá; Tonicapán. Southern Mexico.

Leaf 9-30 cm. long, 0.8-2.5 cm. broad; petiole 3.5-10 cm. long; abaxial surface of lamina amply scaly, but the scales never crowded, the circular, peltate ones commonly 0.2-0.4 mm. in diameter.

Polypodium peltatum var. **peltatum**. *P. polylepis* Roem. ex Kunze, Linnaea 13: 131. 1839. *Drynaria vestita* Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 271. 1850-52. *Pleopeltis polylepis* Moore, Index Fil. 348. 1862.

Apparently known in Guatemala only from two collections: *Lehmann 1559*, undesignated locality, 3,000-4,000 m.; and *Maxon & Hay 3673*, Volcán de Agua, Sacatepéquez, alt. 2,700-3,000 m.; otherwise only occurring in Mexico, usually epiphytic.

Leaf 6-12 (-18) cm. long, 0.5-1.2 (-1.7) cm. broad; petiole 0.5-4 (-7) cm. long; abaxial surface of lamina densely covered with scales, these approximate to imbricate, often completely obscuring the tissue, the circular, peltate ones commonly 0.4-1 mm. in diameter.

Polypodium percussum Cav. Descr. Pl. 243. 1802. *Pleopeltis perculsa* (Cav.) Hook. & Grev. Icon. Fil. t. 67. 1828. *Phlebodium perculsum* (Cav.) J. Sm. J. Bot. (Hooker) 4: 59. 1841. *Drynaria perculsa* (Cav.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 270. 1850-52.

In forests, on tree trunks or, rarely, on rocks, sea level to 800 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Izabal; Petén. Southern Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Rhizome long-creeping, 0.8-2 mm. thick, densely scaly, the scales commonly of 2 kinds, minute, castaneous to blackish, appressed, circular ones, and these often completely hidden by much larger (to 3 mm.), flaccid, subappressed or spreading ones, the latter lanceolate, subentire, nonclathrate, flaccid, tawny to orange, often castaneous at point of attachment; leaves coriaceous, opaque, widely spaced, petiolate, essentially monomorphic (sterile lamina sometimes somewhat broader); petiole 0.5-3 cm. long, somewhat flattened, yellowish, amply provided with minute, circular, dark or dark-centered scales; lamina simple, entire, 7-27 cm. long, 1-3.5 cm. broad, commonly long-acuminate, decurrent at base, narrow-elliptic, costa on both sides prominulous and lighter in color than the leaf tissue, lamina surface essentially naked adaxially, minutely peltate-scaly abaxially, the scales widely scattered, 0.1-0.3 mm. broad, circular (or some

ovate), subentire to ciliate, whitish with a castaneous or orange center; veins immersed and obscure (sometimes even when held to light), copiously anastomosing, only a few areoles containing free veinlets, these variously directed; sori large, circular to ovoid, rather deeply impressed in the tissue, commonly borne nearly the length of the lamina; paraphyses copious, filiform, ferruginous to castaneous, forming dense masses around the sporangia.

Polypodium pleolepis Maxon & Copel. in Copel. Univ. Calif. Publ. Bot. 19: 293. 1941.

Thus far apparently known only from two collections, the type: Baranca del Rubelcruz, Depto. Alta Verapaz, altitude 3,000 ft., *Tuerckheim s.n.* (ed. Donn.-Sm. 673), and *Donnell-Smith 1557*, from the type locality.

Rhizome long-creeping, 1.5-3 mm. thick, abundantly scaly, the scales 2-3 mm. long, lanceolate, acute to attenuate, ferruginous to orange, essentially concolorous, with erose-ciliate margins, subclathrate; leaves monomorphic (or the sterile pinnae slightly broader), long-petiolate; petiole 10-16 cm. long, longer than the lamina, abundantly scaly, yellowish or dark brown, flattened or rounded abaxially, sulcate adaxially, narrowly marginate toward the apex; lamina 3-lobate to deeply pinnatisect or pinnate, chartaceous or subcoriaceous, 9-13 cm. long and nearly as broad, terminating in a coniform, apical segment, naked adaxially, abaxially scaly, the scales abundant but scattered, of 2 kinds, ovate-acuminate and circular-peltate, 0.3-0.6 mm. broad, bicolorous, orange to castaneous, the margins whitish to tawny and conspicuously erose-lacerate to ciliate; lamina segments (or pinnae) 1-3 pairs, elliptic or lanceolate, acute, 5-7 cm. long, 0.8-2 cm. broad, 4-7 times as long as broad, sessile or subsessile or, when adnate, joined by a broadly rounded to squarish sinus, the margins plane, entire or broadly and obscurely crenulate; veins obscure, somewhat phlebotoid, with 2 or 3 irregular series of areoles, some of these with 1-2 free, included veinlets which are variously directed; sori superficial, borne in a single line on each scale of the costa, oblong or ellipsoid, peltate scales rare or lacking among the sporangia.

Subgenus POLYPODIUM

Plants commonly epiphytic, but also frequently epipetric or terrestrial; rhizome long- or short-creeping, rarely ascending, stout to thin and delicate, scaly, the scales broad to filiform, glabrous to variously pubescent or setose, distinctly clathrate or not; leaves commonly small to medium-sized, or sometimes to over 1 m. long, articulate to the rhizome (rarely obscurely so), subfasciculate to remote, commonly long-petiolate; lamina (at least in ours) pinnatifid to (rarely) 3-pinnate-pinnatifid, glabrous to pubescent or scaly; segments or pinnae obtuse to acute or attenuate, entire to crenate or serrate, in a few species decompound, but the ultimate segments never spinulose; venation free, or if areolate then most of the areoles bearing a single, free, excurrent veinlet; sori discrete, round or oblong to ovoid, superficial to (occasionally) impressed, 1- to many-seriate between costa and segment margin, each sorus borne on or near the tip of a vein or veinlet; paraphyses lacking or, if present, filiform to somewhat clavate or, occasionally, peltate or ciliate to stellate; spores monolete, rarely globose, commonly bilateral and often reniform, lacking perine.

As herein construed the subgenus *Polypodium* contains not only those "typical" species of the genus which have the veins free, and the lamina pinnatifid to pinnate (with a few exceptions) and essentially lacking scales, but also those species of the genera or subgenera *Goniophlebium* and *Marginaria*. The latter contains species which differ in no significant way from *Eupolypodium* except that laminar tissue is quite scaly. "Goniophleboid" species are those in which the vein branches merge to form one or more series of areoles, with most areoles containing a free, excurrent veinlet on many of which are borne the sori. Unfortunately this feature is frequently inconsistent, so that a number of species are to be found where free and goniophleboid venation occurs on the same leaf. The following key contains two species which must be "double-keyed" for this reason.

The subgenus as circumscribed here is cosmopolitan and contains about 100 species. The greatest concentration of species occurs in the neotropics, from southern Mexico to the equator.

- a. Lamina scaly on both the axes and the leaf tissue between axes, the scales commonly abundant and conspicuous (in a few species few and minute).
 - b. Lamina pinnate-pinnatifid to 3-pinnate-pinnatifid.
 - c. Leaves subdistant, 2-4 cm. long; rhizome scales minute (0.1-0.2 mm.), lustrous black, or often with light-brown centers. *P. fallax*.
 - c. Leaves crowded, 12-36 cm. long; rhizome scales mostly over 10 mm. long, tawny to light brown (occasionally with a dark-brown dot at point of attachment).
 - d. Lamina pinnate-pinnatisect to occasionally 2-pinnate-pinnatifid; ultimate segments 0.8-1.2 mm. broad, with sori scarcely or not projecting beyond segment margins. *P. lindenianum*.
 - d. Lamina 3-pinnate or 3-pinnate-pinnatifid; ultimate segments 0.3-0.6 mm. broad (so narrow that most sori project well beyond the margins). *P. friedrichsthalianum*.
 - b. Lamina pinnatifid to simply pinnate.
 - e. Rhizome scales essentially concolorous, though often with a dark spot at point of attachment.
 - f. Rhizome scales filiform and hair-tipped; lamina (7) 9-20 cm. broad; veins forming a row of costal areoles. *P. lepidotrichum*.
 - f. Rhizome scales broad and flaccid; lamina 1.5-6.5 (8) cm. broad; veins free.
 - g. Petiole nearly as long as, to longer than, the lamina; sori commonly medial between costa and segment margin. *P. platylepis*.
 - g. Petiole $\frac{1}{2}$ - $\frac{1}{4}$ the length of the lamina; sori commonly supramedial to submarginal.
 - h. Scales ample to abundant on surface of segments adaxially, and often completely obscuring the entire surface abaxially; pinnae mostly subequilateral (dilated about the same on each side) at base; petiole neither alate nor marginate. *P. furfuraceum*.
 - h. Scales lacking (or rarely few and scattered) on surface of segments adaxially, abundant but seldom obscuring the tissue abaxially; pinnae mostly inequilateral at base, strongly dilated acroscopically, but excavate and

- nearly cuneate basiscopically; petiole commonly narrow-olate to marginate. *P. cryptocarpon*.
- e. Rhizome scales bicolorous, many (if not all) of them with broad, castaneous to blackish centers or at least a blackish, percurrent median stripe.
- i. Scales minute and inconspicuous, ample to scattered on abaxial surface of segments.
- j. Leaves crowded or subfasciculate on rhizome, subdimorphous, fertile ones narrower and/or with longer petioles; petiole (at least in ours) alate or marginate for most of its length. *P. remotum*.
- j. Leaves well-spaced on rhizome, essentially monomorphous; petiole nonalate (or inconspicuously alate or marginate near base of lamina).
- k. Rhizome scales (1) 2-4 mm. long, most of them appressed and pointed toward the growing tip, the blackish central portion commonly as broad as (or broader than) each of the plane or undulate brown margins; plants growing at (1,400) 2,100-3,600 m. *P. montigenum*.
- k. Rhizome scales 0.5-1.5 (2) mm. long, most of them spreading and oriented in various directions, the black median stripe filiform, much narrower than the crispate margins; plants growing at 1,000-1,500 m. *P. plebeium*.
- i. Scales copious and conspicuous on segment surface, at least abaxially.
- l. Rhizome scales circular or circular-ovate, 1-2 times longer than broad, predominantly black, with narrow brown margins. *P. sanctae-rosae*.
- l. Rhizome scales elongated, commonly 4-10 times longer than broad, whitish to pale brown, commonly with narrow, castaneous to blackish centers or a linear, black, percurrent median stripe.
- m. Lamina with (12) 15-36 pairs of segments; rhizome scales attenuate, mostly spreading at least at their tips. *P. rosei*.
- m. Lamina with 3-13 (16) pairs of segments; rhizome scales acute or acuminate, mostly appressed.
- n. Petiole commonly longer than the lamina; sori never impressed in the tissue. *P. thyssanolepis*.
- n. Petiole shorter than (or sometimes equaling) the lamina; sori deeply impressed, or sometimes superficial [*P. polypodioides*].
- o. Scales on abaxial surface of segments predominantly acicular, from an abruptly dilated base. *P. polypodioides* var. *aciculare*.
- o. Scales on abaxial surface (but not necessarily the segment margins) circular to ovate or lanceolate, obtuse to acuminate, the base dilated (if at all) only gradually.
- p. Scales of adaxial surface essentially lacking; scales of abaxial surface with margins subentire to serrulate; veins free or forming only a partial series of costal areoles. *P. polypodioides* var. *michauxianum*.
- p. Scales of adaxial surface sparse to ample; scales of abaxial surface mostly with margins strongly serrulate to fimbriate-serrulate; veins forming a nearly complete series of areoles on each side of costa. *P. polypodioides* var. *polypodioides*.
- a. Lamina lacking scales, or in some species with scales scattered along the rachis abaxially.
- q. Veins all free or, in a few species, with an interrupted line of areoles on each side of the costa.

- r. Lamina pinnatisect, pectinate; segments linear or deltoid-linear, all adnate (rarely a few proximal ones discrete); rachis dark reddish brown to blackish.
- s. Rhizome scales broadly ovate or cordate, often nearly as broad as long, mostly appressed.
 - t. Rhizome scales orange or tan; sporangia amply and conspicuously setose. .
P. ferrugineum.
 - t. Rhizome scales dark brown to blackish (or with black centers); sporangia naked or sparsely and inconspicuously setose. *P. alfredii.*
- s. Rhizome scales filiform to narrowly deltoid-lanceolate, obviously longer than broad, mostly spreading (especially those near petiole base).
- u. Rachis and petiole black; rachis scales present, although sometimes sparse, filiform, and inconspicuous.
 - v. Basal segments scarcely reduced, but strongly deflexed; rachis scales filiform, from a dilated base, usually few and inconspicuous.
P. atrum.
 - v. Basal segments (and often a few others) somewhat to very strongly reduced, not or only slightly deflexed; rachis scales narrow-deltoid to ovate, mostly conspicuous.
 - w. Rachis scales broad, mostly subcordate at base and acuminate at apex; veins 1-forked. *P. plumula.*
 - w. Rachis scales narrow-deltoid, often with a dilated, usually hastate base; veins 1- to mostly 2-forked. *P. dispersum.*
- u. Rachis and petiole reddish brown; rachis scales essentially lacking or, if present, so minute as to escape detection.
- x. Basal segments not reduced or, if so, linear or narrow-oblong, not triangular or vestigial.
 - y. Leaves (35) 50-140 cm. long, 8-20 cm. broad; segments with tissue glabrous between costa and margin; sporangia naked.
P. bolivianum.
 - y. Leaves 8-35 cm. long, 2-5 cm. broad; segments strigose throughout; sporangia mostly setose. *P. hygrometricum.*
- x. Basal segments (and usually the next several pairs) strongly reduced to mere auricles, these often broadly triangular, or vestigial and much broader than long.
 - z. Segments minutely pilose in the area surrounding each sorus; petiole commonly 7-15 cm. long; larger segments commonly (4) 5-10 cm. long. *P. ptilodon* var. *caespitosum.*
 - z. Segments essentially glabrous around the sori; petiole commonly 2-5 cm. long; larger segments commonly 2-4 cm. long. *P. consimile.*
- r. Lamina pinnate, or if pinnatisect then not or scarcely pectinate; pinnae or segments mostly lanceolate to deltoid-lanceolate, all of them (or at least some proximal ones) discrete; rachis stramineous to medium brown (very rarely reddish brown).
- aa. Lamina segments discrete and, at least the proximal ones, distinctly narrowed (attenuate to oblique) on both sides at base.
 - bb. Lamina glabrous; sporangia glabrous. *P. fraternum.*
 - bb. Lamina pubescent, at least on the costae; sporangia setose or setulose. .
P. adelphum.
- aa. Lamina segments joined at the rachis, or if discrete then either adnate, truncate or broadly rounded at base; sori medial to inframedial.

- cc. Lamina segments (except the subapical ones) abruptly narrowed at base, truncate to broadly rounded, not or scarcely adnate, sometimes subpetiolate.
- dd. Lamina abundantly pubescent (or short-puberulent) on axes, veins, and leaf tissue on both surfaces; rhizome scales strongly plicate above the base, the margins conspicuously setose. *P. plectolepis*.
- dd. Lamina glabrous between the veins (sometimes ciliate on segment margins); rhizome scales essentially plane, with margins entire or remotely and minutely denticulate.
- ee. Lamina glabrous abaxially; pinnae mostly opposite, with base equally rounded. *P. aequale*.
- ee. Lamina pubescent on costae (and often veins) abaxially; pinnae alternate, with bases commonly tapering unequally (broadly rounded or truncate acroscopically, but cut more obliquely basiscopically). *P. subpetiolatum*.
- cc. Lamina segments (pinnae) not or scarcely narrowed at base, all of them (except rarely the basal ones) broadly adnate on both sides.
- ff. Segment margins biserrate or crenulate-serrate (sometimes obscurely so), the serrations separated by an acute sinus; sori round.
- gg. Segment margins conspicuously biserrate; tissue between veins glabrous. *P. fissidens*.
- gg. Segment margins crenulate-serrate (often obscurely so); tissue between veins commonly puberulent (although the trichomes sometimes deciduous). *P. christensenii*.
- ff. Segment margins entire to sinuate or undulate, or broadly crenate with rounded sinuses; sori mostly elongated.
- hh. Lamina abruptly reduced to a subconform apical segment (which is adnate to the ultimate lateral segment) and pubescent only on the adaxial side of rachis and costae, otherwise glabrous. *P. rhachipterygium*.
- hh. Lamina gradually reduced to a pinnatifid apex and commonly pubescent on axes and veins of both surfaces, and sometimes the segment margins.
- ii. Proximal 3-4 pairs (and especially the basal pair) of pinnae somewhat to strongly reduced; pinnae dilated at base, or at least not constricted. *P. hartwegianum*.
- ii. Proximal pinnae not reduced, or only the basal pair slightly reduced; pinnae commonly somewhat to strongly constricted at base (at least on the basiscopic side).
- jj. Pinnae margins entire (or weakly sinuate); rhizome scales basifixed, not or scarcely pubescent; plants growing at sea level to 800 m. *P. sororium*.
- jj. Pinna margins strongly sinuate or undulate to deeply crenate; rhizome scales peltate, usually densely comose-pubescent at or around the base; plants growing at 1,500-3,200 m. *P. longepinnulatum*.
- q. Veins forming one or more complete series of areoles between costa and each segment margin.
- kk. Pinnae (segments) joined along the rachis, or if discrete, then most of them broadly adnate or decurrent.

- ll. Lamina glabrous throughout, or in some species puberulent only on the axes.
 - mm. Sori elongated; lamina segments widely spaced, most of them connected by a conspicuous wing which runs the length of the rachis. *P. rhachipterygium*.
 - mm. Sori essentially round; lamina segments (pinnae) crowded, or if some proximal ones subdistant then not connected by a conspicuous wing.
 - nn. Pinnae inequilateral at base, strongly surcurrent acroscopically, slightly dilated or perpendicular to the rachis basiscopically; rhizome scales mostly bicolorous, castaneous to blackish, but lighter brown toward margins. *P. loriceum*.
 - nn. Pinnae subequilateral at base (or rarely a few proximal pinnae surcurrent acroscopically); rhizome scales concolorous, pale to dark brown.
 - oo. Rachis and costae glabrous; rachis reddish to reddish brown (at least abaxially). *P. rhodopleuron*.
 - oo. Rachis and costae densely (though minutely) puberulent adaxially; rachis yellowish, or very rarely reddish brown. ... *P. plesiosorum*.
- ll. Lamina puberulent (sometimes minutely so) on axes, veins, and tissue, at least abaxially.
 - pp. Rhizome scales 5-12 mm. long, gray-brown to blackish, iridescent, filiform and hair-tipped, conspicuously clathrate; lamina essentially pinnate and the pinnae mostly falcate. *P. dissimile*.
 - pp. Rhizome scales 1-3 mm. long, tawny to orange or dull brown (and often bicolorous), narrow-deltoid to lanceolate-attenuate; not or scarcely clathrate; lamina deeply pinnatisect (rarely pinnate at very base) and the segments mostly straight.
 - qq. Petiole reddish brown at least abaxially; rhizome scales mostly bicolorous (tawny with dark brown centers), lanceolate-attenuate, appressed, but tips often spreading. *P. fuscopetiolatum*.
 - qq. Petiole yellowish; rhizome scales mostly concolorous (tawny to orange or dull brown), ovate to narrow-deltoid, most of them closely appressed, the tips not or seldom spreading. *P. hispidulum*.
- kk. Pinnae stalked or sessile, narrowed at base, not adnate (or rarely a few distal ones adnate).
 - rr. Lamina pubescent throughout; pinna margins minutely to deeply crenate or crenate-serrate. *P. plectolepis*.
 - rr. Lamina glabrous (sometimes sparsely scaly on rachis); pinna margins entire.
 - ss. Sori in a single series between costa and each pinna margin.
 - tt. Pinnae 0.7-1.3 cm. broad; rhizome scales narrow and hair-tipped, distinctly clathrate with lumina large and clear. *P. antillense*.
 - tt. Pinnae (1.5) 2-5 cm. broad; rhizome scales broad, not hair-tipped, not or scarcely clathrate. *P. lowei*.
 - ss. Sori in (1) 2-5 series between costa and each pinna margin (or if uniseriate then at least a partial series beyond the complete series).
 - uu. Sori in 3-4 (5) series between costa and each pinna margin; rhizome scales mostly appressed, 1-2.5 mm. long, and nearly as broad. *P. fraxinifolium*.
 - uu. Sori in rarely more than 2 series between costa and pinna margin; rhizome scales spreading (at least at the tips), 3-6 mm. long, ovate-acuminate to linear and attenuate. *P. triseriale*.

Polypodium adelphum Maxon, Contr. U.S. Natl. Herb. 8: 275. 1903 (type from Chiapas, Mexico, *Ghiesbreght 244*, in part).

In forests, on tree trunks, stumps or rarely on rocks, 1,800-2,600 m.; Baja Verapaz; Chimaltenango; Huehuetenango; El Quiché; Sacatepéquez. Mexico; Honduras.

Plants epiphytic, rarely epipetric, rhizome creeping, densely scaly, the scales 4-8 mm. long, bright orange, tawny, or brown, mostly spreading, flaccid, ovate-acuminate to lanceolate-attenuate, the margins subentire to minutely and remotely denticulate, usually comose at base with castaneous, filiform trichomes; leaves approximate to widely spaced, 20-66 cm. long, (8) 12-24 cm. broad, petiolate; petiole 8-20 cm. long, stramineous to light brown, glabrous or sparsely pubescent; lamina pinnate, oblong-deltoid, terminating in a subconform apical segment (this often lobed or pinnatifid at base), not or scarcely reduced at base, the tissue thin-herbaceous, glabrous to amply pubescent on the leaf tissue, sparsely to amply strigose on the costae (at least adaxially); pinnae 8-20 pairs, subdistant, lanceolate or linear-lanceolate, narrowly acute or subacute, the margins broadly and faintly crenulate to crenate, cuneate to obliquely rounded at base, distal ones usually adnate, proximal ones very short-petiolate; veins 3- to 4-forked, free; sori round, in a single, mostly medial line between costa and pinna margin; sporangia sparsely to amply setose or setulose.

Polypodium aequale Maxon, Contr. U.S. Natl. Herb. 8: 273, t. 61. 1903.

In forests, on tree trunks, 1,000-2,200 m.; Baja Verapaz; Escuintla; Guatemala; El Quiché (type from San Miguel Uspantán, *Heyde & Lux s.n.* [ed. Donn.-Sm. 3263-B]); Honduras?

Plants epiphytic; rhizome creeping, densely scaly, the scales 3-6 mm. long, brown to bright orange, appressed to spreading, ovate-acuminate or lanceolate, the margins entire, usually comose at the peltate base with castaneous, filiform trichomes; leaves approximate to subdistant, 30-48 cm. long, 9-18 cm. broad, petiolate; petiole 12-20 cm. long, stramineous to pale brown, essentially glabrous; lamina pinnate, oblong-deltoid, terminating rather abruptly in a pinnatifid apex, not or scarcely reduced at base, the tissue thin- to firm-herbaceous, essentially glabrous throughout, except puberulent on the costae adaxially; rachis glabrous abaxially or with a few, scattered, filiform scales, adaxially puberulent; pinnae 12-18 pairs, approximate to subdistant, mostly opposite, oblong or oblong-lanceolate, acute or subacute, margins subentire to obscurely crenulate-serrate, broadly and equally rounded to subcordate at base, subapical ones adnate, the rest sessile or subsessile; veins 2- to 3-forked, free, or often a few of them with branches merging to form costal areoles; sori round, in a single, medial to mostly inframedial, line between costa and pinna margin; sporangia naked, or sometimes sparsely setulose.

The species is represented by only a few Guatemalan specimens, although there is a single pinna from Honduras on a sheet at U.S. National Herbarium (*Molina 1354*) which is probably *P. aequale*.

Polypodium alfredii Rosenst. Repert. Spec. Nov. Regni Veg. 22: 15. 1925. *P. tablazianum* Rosenst. *tom. cit.* 14. *P. cyathicola* Copel.

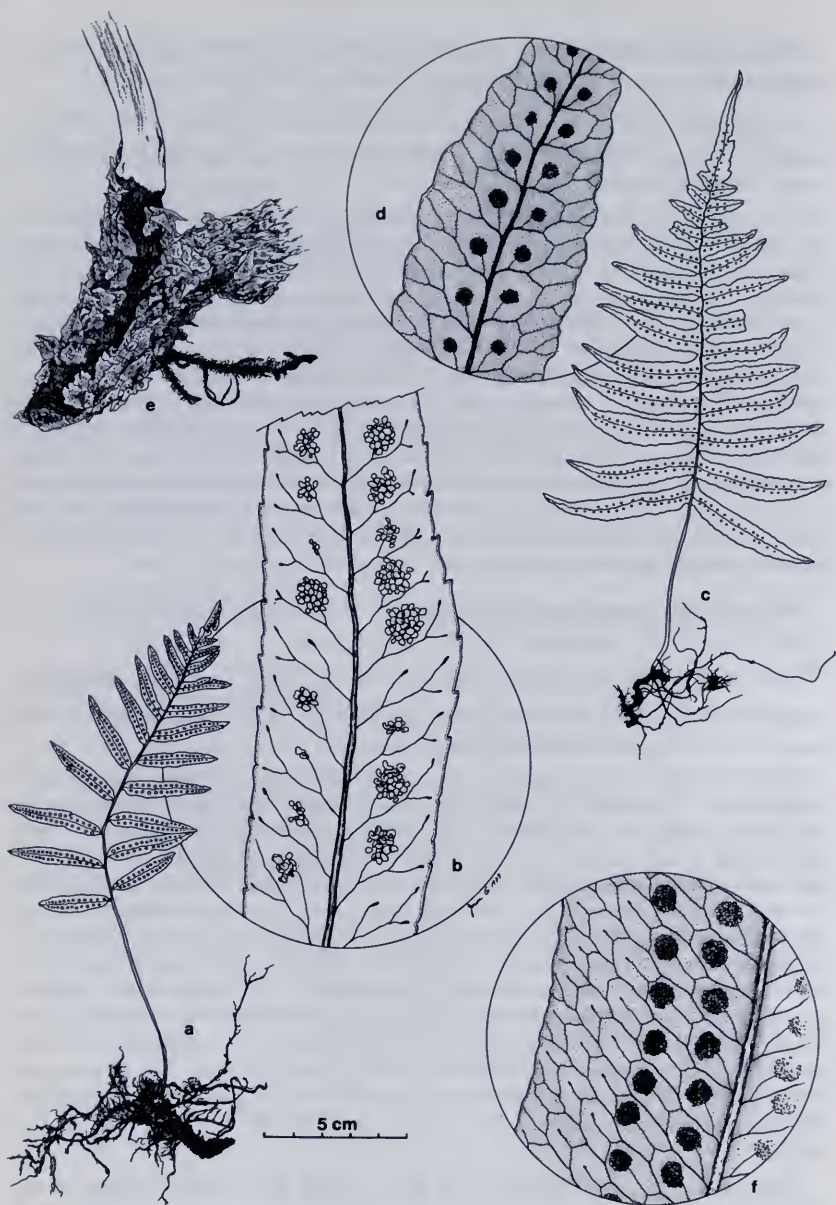


FIG. 66. *Polypodium* subgenus *Polypodium*. a-b, *P. adelphum*: a, habit, $\times \frac{1}{2}$; b, portion of pinna, showing sori and venation, $\times 6$; c-e, *P. loriceum*: c, habit, $\times \frac{1}{2}$; d, portion of pinna showing sori and venation, $\times 3$; e, portion of rhizome showing articulation of petiole, $\times 3$; f, *P. triseriale*, portion of pinna showing sori and venation, $\times 3$.

Univ. Calif. Publ. Bot. 19: 292, t. 43. 1941. *P. cupreolepis* Evans, Ann. Mo. Bot. Gard. 55: 224. 1968.

In forests and wooded ravines, on tree trunks or rocks, 1,000-2,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; Sololá; Zacapa. Mexico to Costa Rica.

Plants epiphytic or epipetric; rhizome short-creeping, densely imbricate-scaly, the scales 1-2 mm. long and often nearly as broad, dark brown or with blackish centers, ovate or broadly elliptic, often cordate at base, acute or obtuse, the margins subentire; leaves approximate or subfasciculate, 12-50 cm. long, 2.5-8 cm. broad, short-petiolate; petiole 2-15 cm. long, reddish brown to blackish, sparsely to amply puberulent or short-pubescent, the trichomes spreading, mostly tawny and pluricellular; lamina closely pectinate, ovate, lanceolate or elliptic, tapering gradually to apex and gradually to abruptly at base, the tissue firm-herbaceous to chartaceous, essentially glabrous, but often with tawny or whitish trichomes on costa and margin; rachis reddish brown to blackish, pubescent, as on the petiole, sparsely to amply scaly (often deciduously so), the scales 0.5-1.5 mm. long, ovate-cordate to narrow-deltoid or -lanceolate, obtuse to acuminate, flat to bullate, orange-brown to castaneous; segments numerous, linear or linear-deltoid, acute, entire, narrowly joined at base (or basal ones discrete), perpendicular to the rachis, or several proximal ones greatly reduced and/or deflexed; veins free, 1-forked; sori round, sparsely paraphysate, in a single, medial to supramedial line between costa and each segment margin; sporangia naked, or sometimes a few of them inconspicuously setulose.

This species is frequently found in herbaria identified as *P. plumula*, *P. pulchrum*, or *P. pectinatum*. Although all species in the complex are superficially similar, the rhizome scales of *P. alfredii* immediately distinguish it from the others. Scales of most of the species are much longer than broad, often filiform, and the narrow tips are conspicuously spreading, especially on those scales surrounding the petiole base. Rhizome scales of *P. alfredii* are often nearly as broad as long, and are tightly imbricate (often clasped together in 3-4 layers). Moreover, their apices are rarely more than subacute, and are never spreading. In Guatemala, only *P. ferrugineum* has such rhizome scales, and these are much lighter in color, commonly orange or very light brown.

Polypodium cupreolepis is supposedly distinguished by the larger and more numerous rachis scales, and perpendicular (*vs.* strongly deflexed) basal segments. In the many dozens of Mexican and Central American collections examined, I found these characters completely inconsistent. For example, many leaves (sometimes from the same rhizome) were seen to have strongly reduced and deflexed lower segments, but the rachis scales were quite numerous, conspicuous, and often bullate.

Polypodium antillense Maxon, Proc. Biol. Soc. Wash. 43: 83. 1930, *nom. nov.* *Goniophlebium acuminatum* Fée, Mém. Fam. Foug. 11: 68, t. 19. 1866 (not *P. acuminatum* Houtt. 1786 nor Sod. 1893).

Thus far known in Guatemala from a single collection; epiphyte in Pansal, Baja Verapaz, 1,000 m., *Tuerckheim II-1687*; and likewise in Nicaragua: epiphyte in forest between Jinotega and Matagalpa, 4,000-4,500 ft., *Bunting & Licht 964*, 1961. Otherwise known only from the West Indies: Cuba, Hispaniola; Jamaica; Guadeloupe; Martinique.

Plants epiphytic; rhizome creeping, often pruinose, 0.6-1.2 cm. thick (often to 1.8 cm. including scales), densely covered with iridescent scales, these 5-15 mm. long, linear to broadly lanceolate, attenuate or hair-tipped, bright brown or gray-brown, distinctly clathrate, spreading (at least at the tips), the margins subentire or often provided with minute, scattered setae; leaves approximate to subdistant, 50-100 cm. long, 20-38 cm. broad, long-petiolate; petiole 12-30 cm. long, yellowish to dark brown, glabrous; lamina pinnate, subdeltoid or deltoid-oblong, scarcely or not reduced at base, essentially glabrous, thin- to firm-herbaceous, terminating rather abruptly in a conform or subconform apical segment, this stalked and entire, or often provided at base with 1-2 pairs of auricles or strongly reduced pinnae; pinnae (10) 12-24 pairs, larger ones 12-20 cm. long, 0.7-1.3 cm. broad, remote, short-stalked to sessile, or a few distal ones slightly adnate, linear-lanceolate, attenuate and often falcate at the apex, the margins entire, sharply or broadly cuneate at base (rarely with a basiscopic auricle); veins evident but often indistinct, not prominulous, primary ones spreading from the costa at a 45-50° angle, flexuous, the secondary (connecting) veins sharply arched to form a single or double series of areoles between costa and pinna margin, each containing a free, excurrent veinlet; sori round, borne one each in the costal areoles, on the tip of the free veinlet; sporangia glabrous.

This may be nothing more than a variety of *P. sessilifolium* Desv. (syn. *P. surucuchense* Hook.?) of South America. Both have the characteristic large, iridescent rhizome scales, the numerous, narrow pinnae, and share most other features. *Polypodium sessilifolium* typically has much larger sori and lamina with thicker texture, and costae often have some large, dark-brown scales on the abaxial side.

Polypodium atrum Evans, Ann. Mo. Bot. Gard. 55: 237, t. 18. 1968 (type from El Cayo District, San Agustín, British Honduras, *Lundell 6639*).

In forests or wooded ravines, on forest floor or on rocks or rocky cliffs, 100-900 m.; Alta Verapaz; Petén. Southern Mexico; British Honduras; Honduras.

Plants terrestrial or epipetric; rhizome short-creeping, rather densely scaly, the scales 2-5 mm. long, ferruginous, mostly spreading, linear or very narrowly deltoid, attenuate or sometimes hair-tipped, the margins subentire; leaves approximate, 20-70 cm. long, 5-12 cm. broad, petiolate; petiole 4-15 cm. long, commonly black, marginate on both sides, sparsely to amply pubescent or glabrescent, sparsely to amply provided with

brown scales; lamina pectinate, broadly to narrowly elliptic, or lanceolate, tapering rather abruptly at both ends, the tissue firm-herbaceous, commonly sparsely whitish-pubescent on both sides, or more abundantly so on the costa and margins; rachis black, copiously pubescent adaxially, sparsely to amply pubescent abaxially and sparsely to amply scaly, the scales brown, linear-deltoid to filiform, mostly hastate and lighter colored at base; segments numerous, linear or linear-oblong, most of them perpendicular to the rachis, the basal pair (and often the next several pairs) scarcely or slightly reduced, but strongly deflexed; veins free, 1- to (usually) 2-forked; sori round, with a few clavate paraphyses, in a single, mostly medial line between costa and each segment margin; sporangia naked or sparsely and minutely setulose.

Polypodium bolivianum Rosenst. Repert. Spec. Nov. Regni Veg. 5: 236. 1908. *P. carpinterae* Rosenst. op. cit. 22: 16. 1925.

In forests or wooded ravines, on tree trunks or occasionally on the forest floor, 800-1,500 m.; Alta Verapaz; Baja Verapaz. Southern Mexico; Honduras; Nicaragua to Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Plants epiphytic or occasionally terrestrial; rhizome long-creeping, scaly, the scales dark brown to ferruginous, 1-3 mm. long, narrow-deltoid, often attenuate, somewhat to densely pubescent at base, and here the margins commonly ciliate; leaves approximate, (35) 50-140 cm. long, 8-20 cm. broad, petiolate; petiole 10-30 cm. long, sublustrous, reddish brown, sparsely and minutely puberulent, scales commonly lacking except at very base; lamina broadly pectinate, lanceolate, tapering gradually to apex, scarcely or not reduced at base, chartaceous to subcoriaceous, commonly drying dark, gray-green (especially adaxially), somewhat strigose on costae and segment margins but essentially glabrous on the tissue between; rachis reddish brown, densely strigose adaxially, sparsely strigose or glabrescent abaxially, scales essentially lacking; segments numerous, linear or linear-deltoid, straight to subfalcate, larger ones 5-10 cm. long, 0.6-1.2 cm. broad, mostly perpendicular to the rachis (rarely the basal pair slightly deflexed), not at all or only slightly reduced toward the base; veins free, mostly 2- to 3-forked, occasionally a few branches merging to form some costal areoles; sori round, with a few clavate paraphyses, in a single, medial to supramedial, line between costa and each segment margin, with some minute, acicular trichomes clustered around the receptacle (which are obscured as sporangia mature); sporangia naked.

Polypodium christensenii Maxon, Contr. U.S. Natl. Herb. 13: 10. 1909.

In forests, on trees or stumps, 1,600-2,500 m.; Alta Verapaz (type from near Cobán, 1,600 m., *Tuerckheim II-2179*); Baja Verapaz; Chimaltenango; El Progreso; El Quiché.

Plants epiphytic; rhizome long-creeping, densely scaly, the scales 6-12 mm. long, orange or reddish brown, flaccid to spreading, ovate to ovate-attenuate, appressed, often slightly comose at the peltate base, the margins entire; leaves remote, to 1.5 m. long, 10-30 cm. broad, petiolate; petiole to 30 cm. long, stramineous to brown, densely pubescent; lamina pinnate, ovate or deltoid-ovate, gradually tapering to a pinnatifid apex, scarcely or slightly reduced at base, the tissue thin- to firm-herbaceous, densely

pubescent on axes, veins and tissue on both surfaces (sometimes minutely or deciduously so on tissue between the veins); rachis stramineous to olivaceous, amply to densely pubescent; pinnae 10-35 pairs, alternate or subopposite, approximate, narrowly deltoid or deltoid-oblong, acute or subacute, margins crenulate or crenulate-serrate (often obscurely so in the proximal portion), broadly adnate at base, mostly free (or distal ones casually joined); veins free, 3- to 5-forked; sori round, in a single medial line between costa and pinna margin; sporangia naked or sparsely setulose.

This could be confused with *P. puberulum* S. & C. of Mexico, but the latter is a much smaller plant and has strongly setose sporangia and much darker and narrower, pubescent rhizome scales.

Polypodium consimile Mett. Ann. Sci. Nat. Bot. (Paris) V, 2: 253. 1864. *P. consimile* Mett. ex D. C. Eaton, Mem. Amer. Acad. Arts, n.s. 8: 198. 1860, *nom. nud.* *P. pityrolepis* Rosenst. Repert. Spec. Nov. Regni Veg. 22: 16. 1925.

In forests, on tree trunks, 30-350 m.; Alta Verapaz. Hispaniola; Jamaica; Costa Rica; Panama; Colombia; Venezuela.

Plants terrestrial to epiphytic; rhizome creeping, scaly, the scales 1-2 mm. long, narrow-deltoid, reddish brown to deep castaneous, acute or attenuate, often subclathrate (with greatly elongated lumina), entire, sometimes densely comose around the base; leaves crowded to subfasciculate, 25-65 cm. long, 4-10 cm. broad, short-petiolate; petiole 2-5 cm. long, reddish brown, sparsely puberulent and often with a few scattered filiform scales; lamina pectinate, narrow-elliptic or elliptic-lanceolate, tapering gradually to apex and base, firm-herbaceous to chartaceous, the tissue essentially glabrous abaxially, but sparsely and minutely pubescent on the margins; rachis reddish brown, rather abundantly strigose adaxially, sparsely pubescent abaxially, lacking scales; segments numerous, linear-deltoid, straight and mostly perpendicular to the rachis, acute or subacute, larger ones 2-4 cm. long, 0.4-0.8 cm. broad, gradually reduced toward base of lamina, the basal ones and several other pairs reduced to mere auricles, these often broadly triangular, or vestigial and much broader than long; veins free, commonly 2-forked; sori round, with a few clavate paraphyses, in a single, mostly medial, line between costa and each segment margin; sporangia often sparsely setulose.

Ours is the typical variety of the species. The South American var. *pastazense* (Hieron.) Evans differs in its broader lamina and broader, densely comose rhizome scales.

Polypodium cryptocarpon Fée. Mém. Fam. Foug. 8: 88. 1857. *P. skinneri* Hook. Sp. Fil. 4: 214, t. 276B. 1862 (type from unspecified location in Guatemala, *Skinner s.n.*).

In forests and coffee plantations, on tree trunks, 90-1,600 m.; Alta Verapaz; Chiquimula; Escuintla; Izabal; Quezaltenango; Retalhuleu; Sacatepéquez; San Marcos. Southern Mexico; Honduras.

Plants epiphytic; rhizome creeping, 1-3 mm. thick, abundantly scaly, the scales 3-5 mm. long, flaccid, appressed to spreading, tawny to orange (occasionally with a darker spot at point of attachment), deltoid-ovate to lanceolate, broadly or narrowly acute,

margins subentire or minutely erose; leaves crowded to subdistant, 9-32 cm. long, 1.5-5 cm. broad, short-petiolate; petiole 1.5-5 cm. long, much shorter than the lamina, yellowish to reddish brown, narrow-alate or adaxially marginate nearly throughout, densely scaly, the scales 0.5-2 mm. long, circular to ovate, flaccid, whitish to tawny, often with a castaneous dot at point of attachment, the margins erose or erose-fimbriate; lamina pectinate, deeply pinnatisect, or sometimes fully pinnate at base, lanceolate to oblong-lanceolate, gradually reduced to a subconform apical segment which is adnate to the next lateral segments, not or slightly reduced at base, opaque, the texture coriaceous or subcoriaceous, lacking trichomes, but densely scaly adaxially (but the scales seldom completely obscuring the surface), scales lacking, or few and scattered, adaxially; rachis densely scaly; pinnae (segments) numerous, linear, 0.7-2.5 mm. broad, slightly ascending, margins slightly sinuate (especially at segment tip) and commonly strongly inflexed, obtuse or subacute, well-spaced, joined by a broad, rounded to subquadrangular sinus, inequilateral at base, strongly dilated acroscopically, excavate and nearly cuneate basiscopically (thus the costa nearly free of tissue at this point); veins free, obscured by the opaque tissue, not visible even when held to light; sori in a single, supramedial to submarginal series between costa and each segment margin, often so large in comparison with the narrow segments that they project beyond the margin.

The only significant differences between this and *P. furfuraceum* relate to degrees of scaliness of lamina and width or outline of segments. Segments of *P. cryptocarpon* typically are strongly inflexed, which accounts for the extreme narrowness and for the fact that margins are somewhat sinuate and that sori often project beyond them. Constriction of segments and reduction in amount of scales perhaps are related to individual habit of plants, and this might provide stimulus for further study. Nevertheless it would appear that the two taxa differ only infraspecifically.

Polypodium dispersum Evans, Amer. Fern J. 58: 173, t. 27. 1968.

In forests or clearings, on tree trunks or rocky soil, 1,000-1,300 m.; Alta Verapaz; Baja Verapaz. Florida; Greater Antilles; Mexico; British Honduras; Honduras; Colombia; Venezuela; Ecuador; Brazil; Bolivia.

Plants epiphytic, terrestrial, or, outside Guatemala, commonly epipetric; rhizome short-creeping, scaly, the scales 2-5 mm. long, lustrous, ferruginous, mostly spreading, narrow-deltoid, attenuate, margins subentire to remotely and minutely denticulate; leaves approximate, 16-55 cm. long, 2.5-7 cm. broad, petiolate; petiole 3-12 cm. long, commonly blackish, marginate on both sides, sparsely to amply pubescent or glabrescent, often provided (especially at base) with a few narrow-deltoid, brown scales; lamina closely pectinate, lanceolate to elliptic, tapering gradually to apex and rather abruptly at base, the tissue firm-herbaceous to chartaceous, subglabrous, but often with a few, scattered, whitish or tawny trichomes abaxially or along the margin; rachis black, densely pubescent (often completely obscured) adaxially, sparsely to amply pubescent abaxially and at least sparsely scaly, the scales flat, reddish brown, mostly narrow-deltoid from an abruptly broadened, often lighter colored, base, their margins minutely denticulate, or fimbriate at base; segments numerous, linear or linear-deltoid, perpendicular to the rachis or distal ones slightly ascending, basal ones somewhat to rather

strongly reduced and sometimes slightly deflexed; veins free, 1- or 2-forked; sori round, with a few clavate paraphyses, in a single, mostly medial line between costa and each segment margin; sporangia naked or sparsely and minutely setulose, containing 32 spores.

Polypodium dissimile L. Syst. Nat. ed. 10, 2: 1325. 1759, excl. ref. Plukenet (type from Jamaica, *P. Browne s.n.*: LINN. 1251.24). *P. chnoodes* Spreng. Neue Entdeck. 3: 6. 1822. *Marginaria chnoodes* (Spreng.) Presl, Tent. Pterid. 189. 1836. *Goniophlebium chnoodes* (Spreng.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 255. 1852. *Calaguala*.

In forests, on stumps or trunks of trees, 350-1,300 m.; Alta Verapaz. West Indies; southern Mexico; Honduras; Nicaragua; Costa Rica; Panama; Colombia; Venezuela.

Rhizome short-creeping, 0.5-1.2 cm. thick (to 1.8 cm. including scales), densely covered with gray-brown to blackish, iridescent scales, these 5-12 mm. long, filiform and hair-tipped from a broadened (often abruptly dilated) base, conspicuously clathrate, with lumina broad and clear; leaves few, approximate, 25-100 cm. long, (8) 12-28 cm. broad, petiolate; petiole 6-20 cm. long, stramineous to yellow-brown, densely puberulent (at least distally) with short, segmented trichomes; lamina firm-herbaceous to chartaceous, pinnate, lanceolate or deltoid-lanceolate, scarcely reduced at base, very gradually tapering to a pinnatifid apex, pubescent on axes, veins, and leaf tissue (usually densely so abaxially), the trichomes whitish, septate, and often twisted; pinnae 18-32 pairs, larger ones 6-12 cm. long, (0.8) 1-1.8 cm. broad, oblong to deltoid-lanceolate, mostly falcate, subacute to short-attenuate, entire or slightly sinuate, well-spaced (or narrowly joined toward the pinnatifid lamina apex), adnate with both sides commonly perpendicular to the rachis, or often the proximal segments truncate to subcordate on the basiscopic side, the basal pair (or 2 pairs) commonly deflexed; veins mostly evident, primary ones flexuous, usually distinct and somewhat prominulous, secondary (connecting) veins indistinct to obscure, obliquely arching and joining adjacent primary veins to form a series of 2-4 areoles between costa and pinna margin, most or all of the areoles with a free, included, excurrent veinlet; sori round, borne on the tips of the free veinlets, in (1) 2-3 series between costa and pinna margin; sporangia glabrous.

This species has been called *Calaguala* (medicinal fern) in Alta Verapaz and is reputedly used as a headache remedy, by applying the rhizome to the forehead (*vide* L. O. Williams).

David Lellinger, U.S. National Museum, has informed me (*in litt.*) that he believes the name *P. dissimile* had been traditionally, but incorrectly, applied to another species, and some discussion is needed here to clarify the matter. To this end, Dr. Lellinger has graciously permitted me to quote or paraphrase some of his correspondence.

Proctor (Fl. Less. Antill. II: Pteridophyta, p. 329. 1977) pointed out that the type of *P. dissimile* L. is *not* the Plukenet plate as cited by Linnaeus, but is instead a Patrick Browne specimen from Jamaica (LINN. 1251.24). Dr. Lellinger concurs with this typification, but decided, from examination of 1251.24 microfiche, that the true type is

actually a species which had been known as *P. chnoodes*: two rows of sori and conspicuous pubescence on the lamina (including the tissue between the veins). He concluded that "Linnaeus received this specimen the year before, annotated it, and included the character of pubescence in his description that could not have come from the Plukenet plate." *Polypodium dissimile*, in the traditional sense, has free (or casually anastomosing) veins, a single series of sori, and essentially glabrous tissue (at least between the veins). Although the microfiche suggested that LINN. 1251.24 was "*P. chnoodes*," the character of pubescence would not, of course, be evident, so Sellinger asked Dr. A. C. Jermy (British Museum) to verify this from the original specimen in the Linn. Soc. Herb. Jermy later replied that a staff member reported the specimen indeed was pubescent. Therefore, although this recent information makes for a confusing situation, it appears that the conclusions are inescapable. The species described above, and traditionally known as *P. chnoodes*, is in fact *P. dissimile* L. Consequently, the species traditionally accepted as *P. dissimile* (essentially free-veined and glabrous, with sori in a single series between costa and margin) can no longer be so named, but instead must bear the epithet of the next available synonym, *P. sororium* H. & B. ex Willd.

Polypodium fallax Schlecht. & Cham. *Linnaea* 5: 609. 1830. *Micropteris fallax* (S. & C.) J. Sm. *Hist. Fil.* 186. 1875. *P. tuerckheimii* Christ, *Bull. Herb. Boissier* II. 5: 254. 1905 (type from Cubilquitz, Alta Verapaz, *Tuerckheim s.n.* [ed. Donn.-Sm. 7721]).

In forests, on trunks and branches of trees, sea level to 800 m.; Alta Verapaz; Chimaltenango; Izabal. Southern Mexico; British Honduras; Honduras; Nicaragua; Costa Rica.

Plants epiphytic; rhizome long-creeping, slender, 0.2-0.5 mm. thick, provided with minute (0.1-0.2 mm.) tightly appressed scales, these ovate to nearly circular, conspicuously clathrate, shiny and black (sometimes with light-brown centers), and often nearly obscured by rigid, castaneous trichomes which are borne on the rhizome (and frequently on the scales themselves); leaves subdistant, 2-4 cm. long, 0.8-1.8 cm. broad, petiolate; petiole 0.5-1 cm. long, yellowish, often narrow-olate or marginate, lacking trichomes, but provided with scattered, minute, appressed, castaneous to blackish scales; lamina pinnate-pinnatifid, lanceolate, ovate or deltoid-ovate, chartaceous, opaque, lacking trichomes, but amply provided (at least abaxially) with small, orange to castaneous, clathrate scales which are scattered along the axes and leaf surfaces; rachis green, free, or marginate to narrow-olate throughout; pinnae 3-6 (7) pairs, commonly less than 1 cm. long, widely spaced, cuneiform to ovate or obovate, cut deeply or shallowly into 1- to several narrow segments or lobes; veins free, obscured within the opaque tissue, not evident even when held to light; sori commonly 1 to a pinna and borne toward the pinna apex, relatively large, often broader than the segments on which they are borne.

Christ described *P. tuerckheimii* as being exactly intermediate between *P. fallax* and *P. lindenianum* (this judgment apparently based on size and degree of dissection of lamina). A type photograph at U.S. National Herbarium suggested it was nearer *P. fallax*, and an inquiry directed to F. Badré at Muséum National in Paris has confirmed this. Dr. Badré examined the two sheets of type there and very graciously communicated the following: "As far as rhizome scales and frond shape are concerned, the two specimens are *P. fallax*. I have examined . . . one scale of the type, which is clathrate and minute (between 0.1 and 0.2 mm.)." The scales of *P. fallax* are quite distinct from those of *P. lindenianum* and *P. friedrichsthalianum*, and this character by itself is sufficient to separate the former from the other two.

***Polypodium ferrugineum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 36, t. 6, f. 2. 1842.**

Apparently known in Guatemala from a single collection: on bluff, along Río Trapichillo, Dept. Huehuetenango, alt. 1,200-1,300 m., *Steyermark 51131*. Otherwise occurring only in Mexico, mostly on rocks or rocky cliffs.

Plants commonly epipetric; rhizome short-creeping, densely imbricate-scaly, the scales 1-1.5 mm. long and often nearly as broad, orange or tan, ovate or broadly elliptic, acute or obtuse, the margins entire; leaves approximate or fasciculate, 5-30 cm. long, 2-5 cm. broad, short-petiolate; petiole 1-5 cm. long, reddish brown, amply to copiously pubescent, the trichomes tawny or whitish, spreading, pluricellular; lamina closely pectinate, narrowly elliptic, tapering gradually at both ends, or sometimes more abruptly at base, firm-herbaceous, amply pubescent on axes and tissue (especially on the margins), the trichomes like those of the petiole, only longer (to 1 mm. on the rachis); rachis scales scattered and inconspicuous, linear, reddish brown; segments numerous, linear or linear-deltoid, acute, entire, narrowly joined at base (or rarely the basal ones discrete), perpendicular to the rachis or several proximal pairs deflexed; veins free, 1-forked; sori round, sparsely paraphysate, in a single medial line on each side of the reddish brown or blackish costa; sporangia amply and conspicuously setose.

***Polypodium fissidens* Maxon, Contr. U.S. Natl. Herb. 8: 275. 1903.**

In forests or rarely in meadows, on trunks or branches of trees or on moist, rocky slopes, 2,600-3,900 m.; Chimaltenango; Huehuetenango; Quezaltenango; Sololá; Totonicapán. Mexico; El Salvador.

Plants epiphytic or occasionally terrestrial; rhizome long-creeping, often pruinose, densely scaly, the scales 4-7 mm. long, orange or reddish brown, flaccid and mostly appressed, ovate to ovate-acuminate, often somewhat comose at the peltate base, the margins entire; leaves subdistant to remote, 15-55 cm. long, 6-15 cm. broad, petiolate; petiole 6-18 cm. long, stramineous to light brown, pubescent; lamina pinnate, ovate, gradually tapering to a pinnatifid apex, scarcely or slightly reduced at base, the tissue thin- to firm-herbaceous, pubescent on costae and veins on both surfaces, and often somewhat ciliate along the pinna margins; rachis light brown, amply pubescent; pinnae

10-20 pairs, opposite or subopposite, approximate, narrowly deltoid or deltoid-oblong, acute or subacute, broadly adnate at base, mostly free (or distal ones casually joined), margins strongly biserrate; veins free, 2- to 3-forked; sori large, round, in a single, medial line between costa and each pinna margin; sporangia naked or (more commonly) amply setose.

***Polypodium fraternum* Cham. & Schlecht. Linnaea 5: 608. 1830.**

In forests, on tree trunks and branches, and on earthen banks and slopes, 400-1,500 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Petén. Mexico; British Honduras; Honduras.

Plants epiphytic or occasionally terrestrial; rhizome creeping, densely scaly, the scales 2-6 mm. long, bright orange to tawny, appressed to spreading, flaccid, broad-ovate or ovate-attenuate, sometimes pubescent at the base, the margins subentire to erose, leaves approximate, 20-60 cm. long, 10-30 cm. broad, petiolate; petiole 10-22 cm. long, stramineous to light brown, glabrous; lamina pinnate, deltoid to oblong-deltoid, terminating in a subconform apical segment (this rarely with a large basal lobe), not or scarcely reduced at base, the tissue firm-herbaceous to chartaceous, glabrous; rachis stramineous or light brown; pinnae 6-10 (12) pairs, subdistant, lanceolate or linear-lanceolate, narrowly acute, the margins entire to broadly and faintly crenulate, sharply cuneate to attenuate at base, distal ones sometimes adnate, at least the proximal ones very short-petiolate; veins several-forked, free, or occasionally some branches converging near the pinna margin; sori round, in a single, mostly medial line between costa and each pinna margin; sporangia naked.

***Polypodium fraxinifolium* Jacq. Coll. Bot. 3: 187. 1789. *Goniophlebium fraxinifolium* (Jacq.) Moore, Index Fil. lxxiv. 1857.**

In forests, on tree trunks, 900-1,500 m.; Alta Verapaz. Nicaragua; Costa Rica; Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Rhizome long-creeping, 0.3-0.7 cm. thick, amply provided with flaccid, tightly appressed scales, these 1-2.5 mm. long, dark brown to blackish, often with scarious margins, minutely but distinctly clathrate, blunt, broadly ovate, nearly as broad as long; leaves several, rather widely spaced on the rhizome, 40-110 cm. long, 25-44 cm. broad, petiolate; petiole 15-40 cm. long, reddish brown to stramineous, glabrous, or with a few scattered, broad, brown, appressed scales as on the rhizome; lamina pinnate, deltoid or deltoid-oblong, scarcely or not reduced at base, terminating in a conform, usually stalked, apical segment, firm-herbaceous, essentially glabrous, but rachis and costae abaxially often with scattered broad, appressed scales; pinnae 4-10 pairs, larger ones 14-24 cm. long, (1.8) 2.2-3.2 cm. broad, widely spaced, sessile, or proximal ones very short-stalked, lanceolate, attenuate, cuneate at base, not or scarcely adnate, the margins not or scarcely cartilaginous, entire; venation regularly areolate, all veins distinct, but rarely prominulous, primary ones spreading from the costa at a broad (60-70°) angle, strongly flexuous, secondary (connecting) veins obliquely arching and joining adjacent primary veins to form a series of 3-4 areoles between costa and pinna margin, these all nearly identical in size and shape and each containing a single, free excurrent veinlet; sori round, borne on tips of free veinlets, commonly 3- to 4- (5-) seriate between costa and margin; sporangia glabrous.

This and *P. triseriale* are very closely related, differing significantly only in those features used in the key. These are part of a larger complex of neotropical, goniophleboid ferns, including, among others, *P. adnatum* Kze., *P. caceresii* Sod., and *P. giganteum* Desv. Taxa within the complex are presumed to differ in characteristics such as type of rhizome scales, number of sori between costa and pinna margin, width of pinnae, and whether or not a few distal pinnae are adnate to the rachis. Guatemalan specimens of *P. fraxinifolium* (and a few in Costa Rica) seem to differ further in that costae are rather amply provided beneath with small, broad, appressed scales. Elsewhere (and as in *P. triseriale*) scales are lacking on the costae, or are very few and filiform. A thorough study of the entire complex is needed.

Polypodium friedrichsthalianum Kze. Farrnkr. 2: 55, t. 123. 1850 (type reputed to be from an unspecified locality in Guatemala, *Friedrichsthal* 1322).

Except for the questionable type locality, found only in Costa Rica, on tree trunks in forests, thickets, and clearings, 800-1,500 m.

Differs from *P. lindenianum* only in the following: leaves not nearly as large, only to about 25 cm. long; lamina more highly dissected, commonly 3-pinnate or 3-pinnate-pinnatifid; ultimate segments 0.3-0.6 mm. broad, so narrow that most sori project well beyond the segment margins.

There is some doubt that the type was truly collected in Guatemala, especially since the species subsequently has never been found outside of Costa Rica. The type locality was reported by Kunze as simply "Guatemala," without further qualifying data.

This and *P. lindenianum* are very similar, and it may be more appropriate to consider the latter merely a variety of *P. friedrichsthalianum*. In their general aspect, leaf dissection, scale covering, and placement of sori, both are easily separated from most other species of *Eupolypodium*. But they differ from each other only quantitatively, *P. friedrichsthalianum* being merely more delicate, slightly smaller, with more highly dissected lamina and narrower ultimate segments. Indeed, a few specimens of *P. lindenianum* have been examined from southern Mexico in which lamina are subtripinnate, and ultimate segments are quite narrow, and are therefore approximately intermediate between the two species.

Polypodium furfuraceum Schlecht. & Cham. Linnaea 5: 607. 1830.

In forests and wooded ravines, on tree trunks or on rocks or cliffs, 700-2,100 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Huehuetenango; Jalapa; Jutiapa; Petén; El Quiché; Sacatepéquez; San Marcos;

Santa Rosa; Sololá; Zacapa. Mexico; Honduras; El Salvador to Panama; Peru; Bolivia.

Plants epiphytic or occasionally epipetric, rhizome creeping, 1-4 mm. thick, abundantly scaly, the scales 4-6 mm. long, flaccid, appressed to spreading, whitish to orange or brown, sometimes with a darker spot near base at point of attachment, deltoid to deltoid-lanceolate, broadly or narrowly acute, margins subentire to erose or denticulate; leaves crowded to subdistant, 10-37 cm. long, 2-5.5 cm. broad, short-petiolate; petiole 2-9 cm. long, much shorter than the lamina, yellowish to reddish brown, nonalate, densely scaly, the scales 0.5-2 mm. long, circular to ovate, flaccid, white to tawny, commonly with a castaneous dot at point of attachment, the margins erose or erose-fimbriate; lamina pectinate, deeply pinnatisect, or fully pinnate at base, lanceolate to oblong-lanceolate, gradually reduced to a subconform apical segment which is adnate to the next lateral segments, not or slightly reduced at base, opaque, the texture coriaceous, lacking trichomes, but densely scaly abaxially (scales often obscuring the entire surface), sparsely to amply scaly adaxially, the scales like those of the petiole, only smaller; rachis densely scaly; pinnae (segments) numerous, linear, 1.2-4 mm. broad, mostly spreading at a 90° angle, entire, obtuse or subacute, well-spaced, joined by a broad, rounded to subquadrangular sinus, subequilateral at base, dilated about the same on each side, or sometimes more strongly decurrent acroscopically; veins free, obscured by the opaque tissue, not or scarcely visible even when held to light; sori in a single, supramedial to submarginal series between costa and each segment margin, often partially covered by scales.

This and *P. cryptocarpon* are difficult to separate, and they may be only varietally distinct.

Polypodium fuscopetiolatum A. R. Smith, Amer. Fern J. 70: 24. 1980.

In forests or wooded ravines, on tree trunks, logs, rocks, or rocky cliffs, 500-1,900 m.; Guatemala; Huehuetenango; Jalapa; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Suchitepéquez. Southern Mexico; Honduras; El Salvador.

Plants epipetric or epiphytic; rhizome creeping, 0.3-0.6 cm. thick, abundantly scaly, the scales 1-3 mm. long, mostly lanceolate and attenuate, bicolorous, tawny, with broad to very narrow, dark-brown centers, appressed, but the tips often spreading and commonly denticulate or papillate, not or scarcely clathrate; leaves approximate to well-spaced, (8) 15-70 cm. long, (5) 8-22 cm. broad, petiolate; petiole 4-14 (18) cm. long, commonly reddish brown (at least abaxially), lustrous, glabrous or glabrescent; lamina thin- to firm-herbaceous, deeply pinnatisect or rarely pinnate at base, deltoid-ovate or lance-ovate, not or only slightly reduced at base, very gradually tapering to a pinnatifid apex (this often with a subconform terminal segment), the leaf tissue, rachis, and costae densely puberulent (or rarely glabrescent), the trichomes whitish, stiff, rarely over 0.1 mm. long; rachis yellowish or, typically, reddish brown, at least abaxially, lacking scales; segments (8) 12-28 pairs, larger ones 4-10 cm. long, 0.6-1.6 cm. broad, narrowly triangular, mostly straight, subacute to attenuate, entire to obscurely and broadly crenulate, subequilateral at base, adnate with both sides either perpendicular to the rachis or equally dilated, or sometimes the proximal segments surcurrent acroscopically, the basal segments not or rarely deflexed; veins several-forked, distinct to obscure (but

always quite evident when held to light), primary ones flexuous, secondary (connecting) veins indistinct to obscure, obliquely arching and joining adjacent primary ones to form a single series of areoles between costa and segment margin, each areole with a free, included, excurrent veinlet; sori round, borne on the tips of the free veinlets, in a single series between costa and margin; sporangia (at least a few of them) setulose.

The species is very closely related to *P. hispidulum*, and more appropriately might be considered a variety of the latter. These two, along with *P. lasiopus* Kl. of South America, and a few others, form a complex which is in need of closer study. Species of the complex, characterized by deeply pinnatisect, puberulent laminae, and uniseriate sori and areoles, have been separated mainly by differences in scales and by color of axes. But neither of these characters is truly constant. A significant number of specimens of *P. fuscopetiolatum* have been observed with wholly yellowish petioles; and rhizome scales of *P. hispidulum* (especially at petiole base) are sometimes narrower and with somewhat acuminate or attenuate tips.

***Polypodium hartwegianum* Hook. in Benth. Pl. Hartweg. 54. 1840.**

In forests, thickets, and wooded ravines, on tree trunks and branches, rarely on the ground, 1,700-3,300 m.; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa. Mexico; El Salvador.

Plants commonly epiphytic; rhizome long-creeping, densely scaly, the scales 2-5 mm. long, ferruginous to castaneous, appressed to spreading, ovate or ovate-acuminate to linear-deltoid and attenuate, often comose at the peltate base, the margins entire; leaves approximate to subdistant, 25-80 cm. long, 5-15 cm. broad, short-petiolate; petiole 2-18 cm. long, usually $\frac{1}{4}$ the length of the lamina or less, yellow to reddish brown or olivaceous, pubescent or glabrescent; lamina pinnate, narrow-ovate to lanceolate, tapering gradually to a pinnatifid apex, somewhat to rather strongly reduced at base, the tissue thin- to firm-herbaceous, pubescent on both sides on axes, margins, and veins, and often on the tissue between veins; rachis yellowish to light brown, amply pubescent; pinnae numerous, spaced about their width apart, more widely so toward the lamina base, free, or the distal ones casually joined, linear- or lanceolate-deltoid, acute, broadly adnate and often dilated on both sides at base, margins entire to sinuate, the proximal 3-4 pairs, and especially the basal pair, somewhat to strongly reduced; veins free, or a few of them with branches merging toward the pinna margin; sori ovoid to oblong, in a single, usually supramedial line between costa and each pinna margin; sporangia naked or sparsely setose.

***Polypodium hispidulum* Bartlett, Proc. Amer. Acad. Arts 43: 48. 1907.**

In forests, on tree trunks, or rocky slopes or cliffs, 30-1,000 m.; Alta Verapaz; Guatemala; Huehuetenango; Izabal (type from Los Amates, *Deam 117*); Petén; Zacapa. Southern Mexico; Honduras.

Plants epiphytic or epipetric; rhizome creeping, 0.2-0.5 mm. thick, abundantly scaly, the scales 1-3 mm. long, ovate to narrowly deltoid, most of them closely appressed, acute or subacute, the tips not or rarely spreading, tawny to orange or dull brown, mostly concolorous, not or scarcely clathrate; leaves approximate to well-spaced, 12-40 cm. long, 6-12 cm. broad, petiolate; petiole 5-11 cm. long, yellowish, glabrous or glabrescent; lamina thin- to firm-herbaceous, deeply pinnatisect or rarely pinnate at base, deltoid- to lance-ovate, not or only slightly reduced at base, very gradually tapering to a pinnatifid apex (this often with a subconform terminal segment), the leaf tissue, rachis, and costae densely puberulent, the trichomes whitish, stiff, rarely over 0.1 mm. long (but to 0.3 mm. long on the axes); rachis yellowish, lacking scales; segments 6-25 pairs, larger ones 2.5-9 cm. long, 0.4-1.5 cm. broad, narrowly triangular, mostly straight, subacute to attenuate, subentire to obscurely and broadly crenulate, subequilateral at base, adnate with both sides either perpendicular to the rachis or equally dilated, the basal segments sometimes deflexed; veins several-forked, distinct to obscure (but always quite evident when held to light), primary ones flexuous, secondary (connecting) veins indistinct or obscure, obliquely arching and joining adjacent primary ones to form a single series of areoles between costa and segment margin, each areole with a free, included excurrent veinlet; sori round, borne on tips of free veinlets, in a single series between costa and margin; sporangia (most of them) setulose.

This and *P. fuscopetiolatum* are very similar. See treatment of the latter for further discussion. According to Steyermark, this species has been called "Calaguala" (Huehuetenango), and its rhizome boiled and the decoction drunk as a remedy for stomachache.

***Polypodium hygrometricum* Splitg.** Tijdschr. Natuurl. Gesch. 7: 409. 1840. *P. truncatulum* Rosenst. Repert. Spec. Nov. Regni Veg. 9: 343. 1911.

In forests, on trees, rocks, or on the forest floor, 200-1,800 m.; Retalhuleu; San Marcos; Suchitepéquez. Southern Mexico; Honduras; Nicaragua; Costa Rica; Panama; Colombia; Venezuela; Peru; Bolivia.

Plants epiphytic, or occasionally terrestrial or epipetric; rhizome long-creeping, scaly, the scales bright orange to brown, 3-5 mm. long, linear-deltoid, attenuate to hair-tipped, the base often abruptly dilated and ciliate; leaves approximate, 8-35 cm. long, 2-5 cm. broad, short-petiolate; petiole 1-4 cm. long, lustrous, reddish brown, amply to densely whitish-pubescent and occasionally with a few filiform scales; lamina broadly pectinate, elliptic or lanceolate, tapering rather abruptly to apex, somewhat reduced at base, thin-herbaceous to membranaceous, usually drying pale or yellowish green, amply strigose on both surfaces, margins, and axes, the trichomes white or silvery; rachis reddish brown, or sometimes yellowish on the adaxial side, strigose as on the lamina surface, scales (if any) minute and difficult to detect; segments numerous, linear-deltoid or narrow-oblong, mostly subacute, never more than 2.5 cm. long and 0.5 cm. broad, mostly perpendicular to the rachis, the basal pair (and often the next several pairs) somewhat reduced but never vestigial, and always much longer than broad; veins free, 1-forked; sori round, with a few clavate paraphyses, in a single, mostly medial line between costa and each segment margin; sporangia each with 1 or 2 setae.

Polypodium lepidotrichum (Fée) Maxon, Contr. U.S. Natl. Herb. 17: 591. 1916. *Goniophlebium lepidotrichum* Fée. Mém. Fam. Foug. 8: 93. 1857.

In forests, on tree trunks, 1,400-2,500 m.; Alta Verapaz; Zacapa. Southern Mexico.

Plants epiphytic; rhizome creeping, 3-8 mm. thick (though appearing thicker due to dense scale covering), the scales 4-10 mm. long, spreading, orange to reddish brown, filiform and hair-tipped, the margins remotely denticulate; leaves approximate to crowded on the rhizome, (15) 20-65 cm. long, (7) 9-20 cm. broad, long-petiolate; petiole (8) 11-27 cm. long, reddish or grayish brown, abundantly scaly, the scales 3-4 mm. long, spreading, tawny, filiform, hair-tipped, from an abruptly broadened, circular, castaneous or blackish base, the margins setulose; lamina deeply pinnatisect, or fully pinnate proximally, deltoid or oblong-deltoid, ending abruptly in a subconform terminal segment which is adnate to the next lateral segments, not or scarcely reduced at base, opaque, the texture firm-herbaceous to chartaceous, lacking trichomes, but surfaces, margins, and costae abundantly provided abaxially (less so adaxially) with crowded, appressed, bicolorous scales, these 0.5-0.7 mm. broad, castaneous, with whitish, fimbriate margins, many of them with attenuate, often hairlike, tips; rachis abundantly scaly like the leaf tissue, but scales larger, darker, and with longer tips; pinnae (or segments) 8-20 pairs, 5-14 cm. long, 0.4-1 cm. broad, linear, acute, not or seldom crowded, joined by a broad sinus or proximal ones discrete but adnate, dilated on both sides at base, the margins entire and slightly thickened; veins obscured by the opaque tissue, not or scarcely visible even when held to light, forming a single series of areoles on either side of the costa, each with a single, included, excurrent veinlet; sori in a single, nearly medial, series between costa and each pinna margin, often densely surrounded (and sometimes partially covered) by scales, frequently immersed in the tissue and thus appearing raised adaxially.

Polypodium lindenianum Kze. Farrnkr. 2: 83. 1851 (type from San Bartolo, Chiapas, Mexico, *Linden s.n.*). *P. verapax* Christ, Bull. Herb. Boissier II. 5: 253. 1905 (type from Cubilguitz, Alta Verapaz, *Tuerckheim s.n.* [ed. Donn.-Sm. 7726]). *Tis-ce* (Quecchí, Alta Verapaz).

In forests, thickets, or clearings, on tree trunks, 100-2,300 m.; Alta Verapaz; Petén; El Quiché; San Marcos. Southern Mexico; Honduras; El Salvador; Nicaragua; Costa Rica.

Plants epiphytic; rhizome creeping, about 1.5 mm. thick, but often appearing thicker due to the dense covering of scales, the scales 1-4 mm. long, tawny to light brown, sometimes darker at point of attachment, broad, not or scarcely clathrate, the margins minutely and irregularly erose; leaves crowded along the rhizome, 12-36 cm. long, 2.5-8 cm. broad, petiolate; petiole 4-10 cm. long, yellowish to castaneous, provided with abundant, broad, whitish to tawny scales similar to those of the rhizome, often narrow-alate or green-marginate distally; lamina commonly pinnate-pinnatisect (occasionally to 2-pinnate-pinnatifid), lanceolate or elliptic-lanceolate, tapering gradually to a pinnatifid apex, the tissue subcoriaceous, opaque, lacking trichomes, but the surface and axes abundantly scaly abaxially, the scales tawny to orange, with castaneous centers, ovate-acuminate, with ciliate margins; rachis scaly, commonly marginate or narrow-alate

throughout; pinnae 1-4.5 cm. long, numerous, imbricate, commonly joined at base by the narrow rachis wing, dissected nearly to the costa into 3-8 pairs of segments; ultimate segments about 1 mm. broad, entire to remotely, obtusely, and shallowly lobed; veins free, obscured within the opaque tissue, not evident even when held to light; sori commonly on or at the bases of segment lobes, most of them covered (and nearly obscured) by masses of scales, and often as large as, but not projecting over, the edges of segments.

The rhizomes (boiled?) have been reported as a native remedy for stomachache (Alta Verapaz). The species is scarcely distinct from *P. friedrichsthalianum*, under which see further discussion.

Polypodium longepinnulatum Fourn. Mex. Pl. 1: 77. 1872. *P. biauratum* Maxon, Contr. U.S. Natl. Herb. 13: 9. 1909 (type from Baja Verapaz, between Purulhá and Panzal, 1,500 m., *Tuerckheim II-1688*).

In forests and wooded ravines, on tree trunks or on the forest floor, 1,500-3,200 m.; Baja Verapaz; Chimaltenango; Escuintla; Quezaltenango; San Marcos; Suchitepéquez. Southern Mexico.

Plants epiphytic or terrestrial; rhizome long-creeping, densely scaly, the scales 2-5 mm. long, deep orange to dark brown, appressed to spreading, ovate to deltoid-lanceolate, usually densely comose at the peltate base, the margins entire; leaves subdistant, 25-90 cm. long, 9-28 cm. broad, petiolate; petiole 8-25 cm. long, yellowish to reddish brown, glabrous or adaxially puberulent; lamina pinnate, ovate or deltoid-ovate, tapering gradually to a pinnatifid apex, scarcely reduced at base, the tissue firm-herbaceous, amply pubescent on the costae on both sides, and usually sparsely so on veins and pinna margins; rachis yellowish or brown, amply pubescent; pinnae 15-30 pairs, approximate, free, or the subapical ones casually joined, deltoid-oblong, acute, broadly adnate on both sides and often auriculate at base, commonly somewhat constricted just above the adnate base, or basiscopically rather strongly constricted or obliquely angled, margins strongly sinuate or undulate to shallow-crenate with rounded sinuses between crenations, the proximal pinnae not reduced, or only the basal pair slightly reduced; veins free, or a few of them with branches merging toward the pinna margin; sori round to (commonly) ovoid, in a single, usually supramedial line between costa and pinna margin; sporangia naked or essentially so.

Polypodium loriceum L. Sp. Pl. 1086. 1753. *Goniophlebium loriceum* (L.) J. Sm. ex Hook. Gen. Fil. 1840.

In forests and wooded ravines, on tree trunks, 1,300-2,600 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Jalapa; Quezaltenango; El Quiché; San Marcos; Suchitepéquez; Zacapa. West Indies; southern Mexico; Honduras; El Salvador to Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Rhizome creeping, greenish or often pruinose, 0.3-0.6 cm. thick, provided with broad, ovate or lanceolate, flaccid, mostly appressed scales, these 2-5 mm. long, dull brown, usually with castaneous to blackish, clathrate centers, the margins subentire; leaves widely spaced on the rhizome, 32-85 cm. long, 10-22 cm. broad, petiolate; petiole 12-27 cm. long, yellowish to dark brown, glabrous, neither alate nor marginate; lamina firm-

herbaceous to chartaceous, deeply pinnatisect or (at base) pinnate, deltoid- or oblong-lanceolate, scarcely or not reduced at base, very gradually tapering to a pinnatifid apex, the tissue glabrous, the rachis and costae abaxially sometimes sparsely provided with minute trichomes or filiform scales; segments (or pinnae) 12-38 pairs, larger ones 5-12 cm. long, 0.8-1.6 (2) cm. broad, deltoid-lanceolate, mostly falcate, acute or attenuate, subentire or slightly sinuate, inequilateral at base, acroscopically surcurrent, on the basiscopic side slightly dilated or (typically) perpendicular to the rachis, the basal ones commonly reflexed; veins distinct and often slightly prominulous, several-forked, the branches merging to form 1 (2) series of areoles between costa and segment margin, each areole with a free, excurrent veinlet; sori round, borne on the tips of the free veinlets in 1 (2) series between costa and segment margin; sporangia glabrous.

Polypodium lowei C. Chr. Index Fil. 541. 1906 (*nom. nov.* for *P. guatemalense* Hook.) *Phlebodium inaequale* Moore, Gard. Chron. 660. 1855 (type from Guatemala, location undesignated, *Skinner, s.n.*) *Goniophlebium inaequale* (Moore) J. Sm. Cult. Ferns 3: 1857. *Polypodium inaequale* (Moore) Lowe, t. 28. 1866 (not Klf. ex Link, 1833 nor Fée, 1866). *Polypodium guatemalense* Hook. Sp. Fil. 29. 1863 (not Kl. 1855).

In forests or wooded ravines, on tree trunks, or rarely on mossy rocks or rocky slopes, 1,350-3,200 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Jalapa; Quezaltenango; El Quiché; San Marcos; Suchitupéquez; Zacapa. Mexico; Honduras; El Salvador; Nicaragua.

Rhizome long-creeping, pruinose, 0.5-1 cm. thick (to 1.5 cm. including scales), densely covered with ferruginous scales, these 6-8 mm. long, broadly or narrowly deltoid, subentire to lightly erose, the margins often becoming scarious; leaves few, widely scattered along the rhizome; 30-110 cm. long, 20-50 cm. broad, petiolate; petiole 10-25 cm. long, stramineous to light brown, glabrous; lamina pinnate, deltoid or deltoid-oblong, scarcely or not reduced at base, terminating in a conform, usually short-stalked, apical segment, firm-herbaceous to chartaceous, essentially glabrous (rarely sparsely and minutely puberulent on the rachis; pinnae 4-12 pairs, larger ones 12-35 cm. long, (1.5) 2-5 cm. broad, widely spaced, sessile to short-stalked, lanceolate or oblong-lanceolate, attenuate, broadly to narrowly cuneate at base, not or scarcely adnate, the margins cartilaginous and entire; venation copiously reticulate, all veins distinct and slightly prominulous, primary ones spreading from the costa at a broad (70-80°) angle, strongly flexuous; secondary (connecting) veins strongly arched and joining adjacent primary veins, forming a single, large costal areole and several irregular series of 2-4 secondary areoles between costa and pinna margin, some areoles with a free included, excurrent veinlet, the costal areole always with a free veinlet, this bearing the sorus (or sometimes branched below the sorus and reaching the adjacent vein, thus forming a narrow, sterile costal areole); sori large and round, borne in a single series on tips of free veinlets in costal or paracostal areoles; sporangia glabrous.

Superficially, this species has the general aspect of *P. triseriale* and *P. fraxinifolium*, but sori are borne in a single series between costa and pinna margin (whereas in the other two species sori are typically 2- to 5-seriate). More importantly, the venation pattern in *P. lowei* is

rather unique among goniophleboid ferns. The typical condition among the latter is that of a single areole (or a single row) between primary veins, each containing a single, free, excurrent veinlet. But in *P. lowei*, beyond the costal areole the anastomosing of veins becomes frequent and irregular, with two to four rows of areoles between primary veins, all of varying size and shape, and with or without included veinlets. Furthermore, the excurrent veinlet in the costal areole may often branch beneath the sorus, this branch meeting the adjacent primary vein and thus forming another, very narrow, areole between costa and fertile areole.

Polypodium montigenum Maxon, in Yuncker, Field Mus. Nat. Hist. Bot. Ser. 17: 306. 1938.

In forests, or rarely on open slopes, on trunks or branches of trees, occasionally terrestrial, or on rocks or rocky cliffs, 1,700-3,600 m.; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Suchitepéquez; Totonicapán. Southern Mexico; Honduras and El Salvador to Panama.

Plants epiphytic, or occasionally terrestrial or epipetric; rhizome long-creeping, 1.5-5 cm. thick, obscured by masses of scales, these (1) 2-4 mm. long, most of them appressed and oriented toward the growing tip, lanceolate or ovate, bicolorous, tawny to brown with a broad, blackish, percurrent, central portion (this commonly broader than each of the brown margins), the margins erose or erose-fimbriate, sometimes undulate; leaves well-spaced, commonly 10-40 mm. apart, monomorphic, 12-45 cm. long, 5-12 cm. broad, petiolate; petiole 7-24 cm. long, reddish brown, alate or marginate (if at all) only near base of lamina, lacking trichomes, but sparsely to amply provided with scales similar to those of the rhizome; lamina deeply pinnatisect, or fully pinnate toward the base, deltoid or broadly oblong, abruptly reduced to a subconform, adnate, apical segment, not or scarcely reduced at base, firm-herbaceous to chartaceous or subcoriaceous, minutely scaly on rachis and leaf tissue abaxially, the scales 0.1-1 mm. long, circular to ovate and often hair-tipped, commonly castaneous; pinnae (segments) 6-18 pairs, spreading or slightly ascending, acute, joined by a subacute to broadly rounded or subquadrangular sinus, or some proximal ones free, both sides often somewhat constricted near the base and then becoming abruptly dilated, the margins remotely serrulate (at least toward segment apex); veins free, 1- to 3-forked, obscure or indistinct, but usually evident when held to light; sori in a single series and more or less medial between costa and each segment margin.

The species is difficult to separate from *P. plebeium*. The two are practically impossible to distinguish in specimens lacking rhizomes. See treatment of the latter for further discussion.

Polypodium platylepis Mett. in Kuhn, Linnaea 36: 137. 1869 (type from unspecified location in Guatemala, *Skinner s.n.*).

In forests or wooded ravines, on tree trunks or occasionally on limestone outcrops, 1,800-3,300 m.; Baja Verapaz; Chimaltenango; Escuintla; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá. Southern Mexico. Also reported, probably in error, from Colombia.

Plants epiphytic, or occasionally epipetric; rhizome creeping, 1.5-3.5 mm. thick, abundantly scaly, the scales 2-5 mm. long, flaccid, appressed to spreading, tawny to orange (often with a large, dark spot at point of attachment), deltoid-ovate to lanceolate, broadly or narrowly acute, margins subentire to erose; leaves 18-45 cm. long, 2.5-6.5 (8) cm. broad, long-petiolate; petiole (8) 10-25 cm. long, commonly as long as, or longer than, the lamina, reddish brown, nonalate, amply to densely scaly, the scales 0.5-2 mm. long, circular to ovate, flaccid, whitish to tawny, commonly with a large castaneous dot at point of attachment, the margins erose or erose-fimbriate; lamina pectinate, deeply pinnatisect, or sometimes fully pinnate at base, deltoid-lanceolate or oblong-deltoid, gradually reduced to a pinnatifid (sometimes subcaudate) apex, not or scarcely reduced at base, opaque, the texture firm-herbaceous to chartaceous or subcoriaceous, lacking trichomes, but densely scaly abaxially (the scales often completely obscuring the surface), scales lacking or few and scattered adaxially; rachis densely scaly; pinnae (segments) 18-26 pairs, linear or narrowly oblong-lanceolate, 1-5 mm. broad, margins sinuate to minutely crenate-serrate, especially near the apex, plane or rarely inflexed, obtuse to acute, well-spaced, joined by a broad, rounded to subquadrate sinus, subequilateral at base, dilated about the same on either side; veins free, obscured by the opaque tissue, not or scarcely visible even when held to light; sori in a single, usually medial, series between costa and each segment margin.

***Polypodium plebeium* Schlecht. & Cham. Linnaea 5: 607. 1830.**

In forests, on tree trunks, 1,000-1,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Guatemala; Quezaltenango; Sacatepéquez; Sololá; Suchitepéquez; Totonicapán. Mexico; Honduras; El Salvador to Panama.

Plants epiphytic; rhizome long-creeping, 2-5 mm. thick, obscured by masses of scales, these 0.5-1.5 (2) mm. long, mostly spreading and oriented in all directions, lanceolate- or ovate-subulate, bicolorous, tawny to brown with a shiny, black, filiform, percurrent, median stripe (the stripe conspicuously narrower than the brown margins), the margins erose and crispate; leaves well-spaced, commonly 8-30 mm. apart, monomorphic, 15-45 cm. long, 5-15 cm. broad, petiolate; petiole 8-24 cm. long, reddish brown, nonalate (but occasionally marginate near base of lamina), lacking trichomes, but sparsely provided with scales similar to those of the rhizome; lamina deeply pinnatisect, or fully pinnate at the base, deltoid or oblong-deltoid, abruptly reduced to a subconform apical segment which is adnate to the ultimate lateral segments, not or scarcely reduced at base, firm-herbaceous to chartaceous or subcoriaceous, sparsely and minutely (often deciduously) scaly on rachis and leaf tissue abaxially, the scales 0.1-0.4 mm. long, circular to ovate or ovate-attenuate, commonly castaneous; pinnae (segments) 12-20 pairs, linear, spreading or slightly ascending, acute, joined by a subacute to broadly rounded sinus, or some proximal ones free, both sides often somewhat constricted near the base and then becoming abruptly dilated, the margins remotely serrulate (at least toward segment apex); veins free, 1- to 3-forked, indistinct to obscure, but usually evident when held to light; sori in a single series on each side of the costa, medial to inframedial.

Specimens lacking rhizomes are virtually impossible to assign to this species or *P. montigenum*, for rhizome scales are the only truly distinguishing character. Fortunately, in Guatemala, from all collections thus far available, *P. plebeium* appears to be a plant of middle elevations (1,500 m. or less) whereas *P. montigenum* commonly occurs at well over 2,000 m. With the limited material on which Maxon based his original description of the species, *P. montigenum* was also supposed to have the lamina essentially pinnate, with pinnae or segments more widely spaced. But with dozens of collections now available, it is obvious this character is no longer efficacious. Consequently, the single feature of rhizome scales would seem insufficient to warrant separating the two taxa above the varietal level.

Polypodium plectolepis (Fée) Hook. Sp. Fil. 5: 30. 1863. *P. insigne* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 193 (seors. 41). 1849 (not Bl. 1828). *Goniophlebium plectolepis* Fée, Mém. Fam. Foug. 8: 95. 1857 (type from Orizabaa, Mexico, *Schaffner* 187). *P. macrodon* Hook. Sp. Fil. 4: 218. 1862 (not Reinw. 1867) (type from Cobán, Alta Verapaz, *Salvin s.n.*). *P. legionarium* Bak. in Hook. & Bak. Syn. Fil. 337. 1867. *Calaguala*.

On tree trunks in forests or clearings, occasionally on rocks, 600-1,400 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; Sololá. Southern Mexico; Honduras; Nicaragua; Costa Rica; Panama.

Plants commonly epiphytic; rhizome creeping, densely scaly, the scales 3-6 mm. long, orange to ferruginous, mostly spreading, rigid, strongly plicate and acicular, from an abruptly dilated, peltate base, the margins strongly setose; leaves widely spaced, to 1 m. long and 30 cm. broad, petiolate; petiole 7-30 cm. long, stramineous to brown, glabrous or sparsely puberulent; lamina pinnate, deltoid-oblong to -ovate, tapering abruptly to a subconform apical segment (which is usually lobed at base and adnate to the ultimate lateral segment), not or slightly reduced at base, the tissue firm-herbaceous to chartaceous, sparsely to amply pubescent on axes, veins and leaf tissue on both surfaces, but the indument of the leaf tissue often only minutely glandular-puberulent and inconspicuous; pinnae 8-30 pairs, subdistant, deltoid- or oblong-lanceolate, acute to attenuate, the margins minutely to deeply crenate or crenate-serrate, distal ones adnate, the rest free and some of them very short-stalked, broadly rounded to truncate at base; veins 4- to 6-forked, mostly free, or the branches of adjacent ones merging to form a continuous or interrupted line of areoles on each side of the costa; sori round, in a single, commonly inframedial line between costa and pinna margin; sporangia amply to sparsely setose.

The cooked rhizome of *P. plectolepis* is reputed to be used as a treatment for asthma, cancer, and throat infections—thus the common name “calaguala,” or “medicinal fern.”

Polypodium macrodon and *P. plectolepis* have been traditionally separated on the basis of free *vs.* areolate venation. However, this character, often highly questionable as diagnostic in the *Eupolypo-*

dium-Goniophlebium complex, is particularly ineffectual here. Many specimens have been examined in which one pinna may have vein branches merging to form a nearly complete line of costal areoles, and elsewhere on the same leaf another pinna (or the other side of the same pinna) may have veins mostly free. Moreover, no other features can be consistently or effectively employed to delineate two separate entities. In size of lamina and size, shape, and margins of pinnae, the species can be highly variable, but otherwise it is quite well defined. The rhizome scales—acicular, strongly plicate, and setose, from a suddenly and greatly dilated base—are perhaps the most distinctive in the species complex. *Polypodium plectolepis* can also be recognized by its mostly discrete and free pinnae, and by the general pubescence of its surfaces, including the tissue between the veins.

Polypodium sessilifolium Liebm., variously reported from Mexico and parts of Central and South America, has been often confused with *P. plectolepis*. Indeed, they are similar, but rhizome scales of the former are gray-brown to blackish and are distinctly clathrate, with lumina large and clear.

***Polypodium plesiosorum* Kze.** Linnaea 18: 313. 1844. *Goniophlebium plesiosorum* (Kze.) Fée, Mém. Fam. Foug. 9: 24. 1857.

In forests, on trunks of trees, or on wet, mossy rocks or rocky cliffs, 1,300-2,900 m.; Alta Verapaz; Baja Verapaz; Escuintla; Guatemala; Jalapa; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Zacapa. Mexico; Honduras; El Salvador; Nicaragua; Costa Rica; Panama; Venezuela.

Plants epiphytic, or rarely terrestrial or epipetric; rhizome long-creeping, 0.3-0.6 cm. thick, abundantly scaly, the scales 3-5 mm. long and nearly as broad, irregularly ovate or elliptic, pale to dark brown, dull, concolorous, the margins subentire; leaves closely to widely spaced on the rhizome, 14-45 cm. long, (4) 5-12 cm. broad, petiolate; petiole 5-18 cm. long, glabrous, stramineous, or (rarely) light brown, neither alate nor marginate; lamina thin- to firm-herbaceous, deeply pinnatisect or rarely pinnate at base, deltoid or ovate, slightly or not at all reduced at base, very gradually tapering to a pinnatifid, sometimes somewhat attenuate, apex, the tissue glabrous, the rachis and costae glabrous abaxially, but densely (though minutely) puberulent adaxially, lacking scales; rachis yellowish, or very rarely reddish brown; segments 10-20 pairs, larger ones 3-8 cm. long, 0.6-1.4 cm. broad, narrowly triangular, mostly straight, acute to attenuate, entire to sinuate (rarely crenulate), subequilateral at base, both sides either perpendicular to the rachis or equally dilated, the basal pinnae commonly deflexed; veins evident, usually distinct, only rarely slightly prominulous, several-forked, the branches merging to form a single series of areoles between costa and segment margin, each areole with a free, included, excurrent veinlet; sori round, borne on the tips of the free veinlets in a single series between costa and segment margin; sporangia glabrous.

This and *P. rhodopleuron* are scarcely distinct. See treatment of the latter for further discussion.

Polypodium plumula H. & B. ex Willd. in L. Sp. Pl. ed. 4, 5: 178. 1810. *P. pulchrum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 41. 1842 (type from Veracruz, Mexico, *Galeotti 6332*). *Ctenopteris plumula* (H. & B. ex Willd.) J. Sm. Hist. Fil. 185. 1875.

In forests or open places, on tree trunks, rocks, or rocky soil, 200-1,300 m.; Alta Verapaz; Escuintla; Huehuetenango; Jutiapa; Petén; Quezaltenango; Retalhuleu; Santa Rosa; Suchitepéquez; Zacapa. Florida; West Indies; Honduras; El Salvador to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Plants epiphytic, or occasionally terrestrial or epipetric; rhizome short- or long-creeping, rather densely scaly, the scales 1-3 mm. long, ferruginous to castaneous, mostly spreading, linear or very narrowly deltoid, attenuate to hair-tipped, the margins subentire to remotely and minutely denticulate; leaves approximate, 15-50 cm. long, 2.5-7 cm. broad, petiolate; petiole 2-12 cm. long, commonly black, marginate on both sides, sparsely to amply pubescent or glabrescent, often provided with a few brown scales; lamina closely pectinate, linear to narrow-elliptic, tapering gradually to the apex and rather abruptly at base, the tissue firm-herbaceous to chartaceous, often with a few scattered, whitish, or tawny trichomes abaxially or along the margin; rachis black, densely pubescent adaxially, sparsely to amply pubescent abaxially and sparsely to abundantly scaly, the scales broad, conspicuous, and bullate to narrow-lanceolate and flat, orange to dull brown, often subcordate at base and acute to short-acuminate at apex; segments numerous, linear, perpendicular to the rachis, or distal ones slightly ascending, basal ones somewhat to strongly reduced, only rarely slightly deflexed; veins free, 1-forked; sori round, with a few long, clavate paraphyses, in a single, mostly medial line between costa and each segment margin; sporangia naked or sparsely and minutely setulose.

Polypodium polypodioides (L.) Watt, *Canad. Naturalist* II. 3: 158. 1867.

Plants epiphytic or epipetric; rhizome creeping, 1-2.5 mm. thick, densely scaly, the scales 1-4 mm. long, 0.1-0.3 mm. broad, linear or linear-lanceolate, acute, appressed, many of them bicolorous, whitish or tawny to pale brown, with rather broad centers (or sometimes merely a narrow median stripe), the margins subentire to erose-ciliate; leaves well-spaced, 4-20 cm. long, 1.5-4 cm. broad, petiolate; petiole 1-10 cm. long, as long as or (more commonly) shorter than the lamina, yellowish to reddish brown, abundantly scaly, the scales bicolorous, circular to ovate or lance-attenuate, the margins subentire to denticulate or erose-ciliate; lamina deeply pinnatisect, rarely pinnate at base, oblong or deltoid-oblong, abruptly reduced to a subconform, adnate, apical segment, not reduced at base, chartaceous to subcoriaceous, rachis scaly as on the petiole, lamina surface with scales lacking or sparsely to amply scattered on the adaxial surface, these commonly whitish, acicular, from an abruptly broadened, stellate base, scales copious on (and often completely covering) the abaxial surface, circular to ovate-acuminate or acicular from an abruptly dilated base, the margins subentire to fimbriate;

segments 6-13 (16) pairs, linear or narrow-oblong, spreading or slightly ascending, obtuse to subacute, joined by a broadly rounded sinus, subequally dilated on both sides at base, the margins entire; veins obscured by the dense scales and/or opaque tissue, several-forked, free, or the branches merging to form a single, partial or complete row of areoles on each side of the costa; sori superficial to (typically) deeply immersed in the tissue, borne in a single series on each side of the costa.

A number of varieties have been described in this widely distributed species, three of which occur in Guatemala. Of the three, var. *aciculare* is the easiest to recognize, mainly because of the scales on the abaxial surface of segments, which are predominantly spreading and acicular at the tips. Specimens described as var. *michauxianum* are not as easy to separate from the typical variety. The former supposedly differs in the completely scaleless adaxial surface of its segments, and the less dissected margin of its scales on the abaxial surface. Neither of these is a strong character, for there are many intermediate cases where adaxial scales are only a very few, and margins of abaxial scales are somewhere between "denticulate" and "fimbriate."

Polypodium polypodioides* var. *aciculare Weath. Contr. Gray Herb. 124: 33. 1939.

In forests, thickets, and wooded ravines, on tree trunks, logs, or rocks, 800-2,100 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Huehuetenango; El Quiché; Sacatepéquez; Sololá; Zacapa. Mexico; Honduras; El Salvador to Panama.

Segments of lamina with scales sparsely to amply scattered on the adaxial surface, but copiously scaly abaxially, with scales circular to ovate-acuminate, but predominantly acicular from an abruptly dilated base, the margins subentire to serrulate; veins free, or branches occasionally merging to form some costal areoles.

Polypodium polypodioides* var. *michauxianum Weath. Cont. Gray Herb. 124: 31. 1939.

In forests and wooded ravines, on trees, rocks, or rock walls, sea level to 500 m.; Alta Verapaz; Izabal. United States; Mexico; in scattered locations throughout Central America.

Segments of lamina with scales essentially lacking on adaxial surface, but abundantly scaly abaxially, with scales circular or circular-ovate, obtuse to acute (or a few along the segment margin acuminate), subentire to serrulate; veins free, or branches occasionally merging to form some costal areoles.

***Polypodium polypodioides* var. *polypodioides*.** *Acrostichum polypodioides* Sp. Pl. 1068. 1753. *P. incanum* Sw. Prodr. Veg. Ind. Occ. 131. 1788. *Margitaria polypodioides* (L.) Tides. Torreya 5: 171. 1905.

In forests, thickets, and wooded ravines, on tree trunks or rocks, 300-1,500 m.; Chimaltenango; Jalapa; Petén; Zacapa. West Indies; Mexico; Honduras; El Salvador to Panama; northern South America.

Segments of lamina with scales sparsely or amply scattered on the adaxial surface, but copiously scaly abaxially, with scales circular or, more commonly, ovate- to lanceolate-acuminate (or a few along segment margin attenuate), from a gradually dilated base, the margins serrulate to fimbriate-serrulate; veins forming a nearly complete series of costal areoles on each side of the costa.

Polypodium ptilodon Kze. var. **caespitosum** (Jenm.) Evans, Amer. Fern J. 58: 170. 1968. *P. pectinatum* of authors (not L. 1753). *P. pectinatum* var. *caespitosum* Jenm. Bull. Bot. Dept. Jamaica, n.s. 4: 125. 1897.

Apparently represented in Guatemala by a single collection: in low forest, Dolores, Petén, *Contreras 2468*; otherwise, in forests or wooded ravines, commonly on logs or bases of trees, sea level to 1,500 m. Florida; Greater Antilles; Mexico; Honduras.

Plants terrestrial to epiphytic, rarely epipetric; rhizome long-creeping, scaly, the scales 2-5 mm. long, dark brown or reddish brown, narrow-deltoid, often attenuate, entire, somewhat pubescent at base; leaves approximate to subfasciculate, 25-100 cm. long, commonly 6-18 cm. broad, petiolate; petiole commonly 7-15 cm. long, sublustrous, reddish brown or rarely atropurpureous, puberulent, scales lacking or few and filiform near the petiole base; lamina pectinate, broadly lanceolate or elliptic-lanceolate, tapering gradually to apex, more abruptly so at base, firm-herbaceous to chartaceous, the tissue glabrous to sparsely and minutely puberulent abaxially, but always minutely pilose in an area surrounding each sorus; rachis reddish brown, densely strigose adaxially, sparsely pubescent abaxially, scales (if any) minute, filiform, and difficult to detect; segments numerous, linear-deltoid, straight and mostly perpendicular to the rachis, acute or subacute, larger ones (4) 5-10 cm. long, 0.5-1 cm. broad, gradually reduced toward base of lamina, the basal ones (and often the next several pairs) reduced to mere auricles, these often broadly triangular, or vestigial and much broader than long; veins free, (1) 2- to 3-forked; sori round, or occasionally oblong, with clavate paraphyses, in a single, mostly medial, line between costa and segment margin; sporangia often sparsely setose.

The typical and two other varieties of *P. ptilodon* occur in South America. They differ principally in relative length of petiole, lamina, and shape of segments.

Polypodium remotum Desv. Prodr. 232. 1827 (not Baker, 1891). *P. leucosticton* Kze. ex Kl. Linnaea 20: 380. 1847 (not Fée, 1857).

In forests or wooded ravines, on tree trunks or rarely on limestone, 1,150-2,000 m.; Alta Verapaz; El Progreso. Southern Mexico (Chiapas); Nicaragua to Colombia and Venezuela; Ecuador; Peru; Bolivia.

Plants epiphytic, rarely epipetric; rhizome short-creeping to ascending, 3-8 mm. thick, densely covered with a mass of brown-tomentose roots, scaly, the scales 1.5-4 mm. long,

spreading, lanceolate or deltoid-lanceolate, bicolorous, tawny or darker brown with narrow, black median stripe, the margins plane to undulate, strongly erose; leaves crowded to subfasciculate, subdimorphous, 12-60 cm. long, 4-15 cm. broad, the fertile ones commonly narrower than the sterile and their petioles proportionately longer; petiole 4-20 cm. long, yellowish to reddish brown, conspicuously alate or strongly marginate (at least in ours) nearly to base (the wings often deciduous), lacking trichomes, but amply provided with scales like those of the rhizome; lamina deeply pinnatisect, deltoid-ovate to -lanceolate or oblong-lanceolate, gradually reduced to a pinnatifid, often subcaudate, apex, not or scarcely reduced at base, firm-herbaceous to chartaceous, amply filamentous-scaly on rachis abaxially, scales present, but scattered and inconspicuous, on segments; segments 8-20 pairs, linear to narrow-oblong, slightly ascending, obtuse or subacute, well-spaced (or closer on sterile laminae), joined by a subacute to broadly rounded sinus, the margins entire to sinuate or remotely serrulate toward segment apex; veins free, 1- to 2-forked, obscure, but usually evident when held to light; sori in a single series on each side of the costa, and at maturity so large that they often extend from costa to segment margin.

Characteristics of the species, as recognized herein, are fairly constant in Guatemala and southern Mexico, but are not nearly so stable in Costa Rica and Panama and are even more variable in South America. In southern Central America the petiole is not always alate, and may not even be marginate, except near the lamina. In South America, some specimens may lack a petiole wing, and others may have essentially monomorphous leaves. *Polypodium remotum* needs to be more closely studied throughout the range, for it is likely some distinct varieties should be recognized.

Polypodium rhachipterygium Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 191 (seors. 39). 1849. *Goniophlebium rhachipterygium* (Liebm.) Moore, Index Fil. 396. 1862. *P. stenoloma* D. C. Eaton, Proc. Amer. Acad. 8: 618. 1873. *P. donnell-smithii* Christ, Bull. Herb. Boissier II. 6: 291. 1906 (type from Cubilguitz, Alta Verapaz, 350 m., *Tuerckheim s.n.*, ed. Donn.-Sm. 8823).

In forests, on trunks or branches of trees, 100-1,400 m.; Alta Verapaz; Huehuetenango; Izabal; San Marcos. Southern Mexico; Honduras.

Rhizome creeping, 0.2-0.7 cm. thick, amply provided with dark-brown or yellowish brown scales, these 2-3 mm. long, flaccid, mostly appressed, deltoid or ovate, subentire; leaves approximate to subdistant, 40-80 cm. long, 16-28 cm. broad, petiolate; petiole 16-30 cm. long, yellowish to reddish brown, sparsely and minutely puberulent or glabrate, alate (or at least marginate) nearly to the base; lamina pinnate, ovate to broadly or narrowly deltoid, slightly or not at all reduced at base, abruptly reduced to a subconform apical segment which is adnate to the ultimate lateral segments, the tissue glabrous, the rachis and costae commonly minutely puberulent adaxially; pinnae or segments (7) 10-20 pairs, larger ones 10-20 cm. long, 2-2.5 cm. broad, lanceolate to elliptic, acute to attenuate, the margins entire, or sinuate or undulate toward the apex, most of them widely spaced and connected by a conspicuous wing which runs the length of the

rachis; veins distinct, primary ones prominulous or not, several-forked, nearly all free, or few to many with branches merging to form a single series of costal areoles; sori elongated, borne in a single, medial to inframedial line between costa and margin, on the tips of the basal acroscopic branch of each vein; sporangia naked.

Anastomosing of veins is a highly variable condition in this species. In some plants there is nearly an unbroken line of costal areoles, yet just as often the veins may be almost completely free. *Polypodium rhachipterygium* is characterized by the elongated sori, by the broad, widely spaced pinnae, and the (usually) broad wing of tissue along the rachis.

This is closely related to *P. sororium*, and may not be specifically distinct. See treatment of the latter for further discussion.

Polypodium rhodopleuron Kze. Linnaea 18: 315. 1844. *Goniophlebium rhodopleuron* (Kze.) Fée. Mém. Fam. Foug. 9: 24. 1857.

In forests or wooded ravines, on tree trunks, or occasionally on mossy rocks or soil, 500-1,600 m.; Alta Verapaz; Izabal; Quezaltenango; San Marcos. Southern Mexico; Honduras; Nicaragua; Costa Rica; Panama.

Plants epiphytic, or occasionally terrestrial or epipetric; rhizome long-creeping, 0.2-0.6 cm. thick, abundantly scaly, the scales 1-3 (4) mm. long and often nearly as broad, irregularly ovate or elliptic, pale to dark brown, dull, concolorous, the margins subentire; leaves closely to widely spaced on the rhizome, 12-50 cm. long, (4) 5-20 cm. broad, short-petiolate; petiole (2.5) 4-16 cm. long, commonly about $\frac{1}{4}$ the length of the lamina, glabrous, nonalate, and not or scarcely marginate, commonly bicolorous, reddish brown abaxially, yellowish brown adaxially; lamina thin- to firm-herbaceous, deeply pinatisect, or rarely pinnate at base, deltoid or ovate, slightly or not at all reduced at base, very gradually tapering to a pinnatifid, sometimes somewhat attenuate apex, tissue glabrous and often reddish tinged; rachis reddish to reddish brown, this and the costae glabrous; segments 14-28 pairs, larger ones 3-9 cm. long, 0.4-1.2 cm. broad, narrowly triangular to oblong, subacute to attenuate, the margins subentire to broadly and shallowly crenulate, subequilateral at base, both sides either perpendicular to the rachis or equally dilated, or rarely several proximal pairs more strongly dilated acroscopically, the basal pinnae commonly deflexed; veins evident, mostly distinct, often reddish, only rarely slightly prominulous, several-forked, the branches merging to form a single series of areoles between costa and segment margin, each areole with a free, included, excurrent veinlet; sori round, borne on the tips of the free veinlets in a single series between costa and segment margin; sporangia glabrous.

This more appropriately might be considered simply a variant of *P. plesiosorum*, as treated by Christensen in the Index Filicum. The only truly consistent distinction seems to be the always-glabrous condition of the axes in *P. rhodopleuron* vs. the densely but minutely puberulent rachis and costae on the adaxial side in *P. plesiosorum*. The usually reddish rachis, and the red-tinged tissue in the former, are also usually diagnostic, but a few specimens of *P. plesiosorum* have been

observed with this same coloration. The two species, with *P. loriceum*, form part of a complex within the genus, the relationships of which are in need of further study.

Polypodium rosei Maxon, Contr. U.S. Natl. Herb. 17: 594. 1916. *Goniophlebium rosei* (Maxon) Conz. Fl. Taxon Mex. 1: 106. 1939.

Not yet reported from Guatemala, but perhaps to be expected here; otherwise on rocks, cliffs, or rocky ground, or occasionally on tree trunks, in forests, ravines, or roadsides, 900-2,300 m., in Mexico and Honduras.

Plants terrestrial, epipetric, or sometimes epiphytic; rhizome creeping, 2-5 mm. thick, densely entangled with brown-tomentose roots, and covered with scales, these 2-6 mm. long, 0.2-0.8 mm. broad, lanceolate- or linear-deltoid, attenuate, spreading, predominantly bicolorous, tawny to orange or reddish brown, a majority of them with broad to narrow, darker (often blackish) centers or median stripes, the margins setose or ciliate; leaves 10-48 cm. long, 3-10 cm. broad, short-petiolate; petiole 2-16 cm. long, much shorter than the lamina, yellowish brown to castaneous, often completely covered with scales which are similar to those of the rhizome, but usually longer and lighter in color, sometimes whitish; lamina deeply pinnatisect, or fully pinnate toward the base, oblong- or elliptic-lanceolate, gradually or abruptly reduced to a subconform, adnate, apical segment, somewhat to not at all reduced at base, chartaceous or subcoriaceous, rachis and tissue of both surfaces abundantly scaly, often so densely abaxially as to fully obscure the tissue, the scales 1-3 mm. long, linear-deltoid to filiform, hair-tipped, from an abruptly dilated, usually castaneous base, the margins setose, scales of costae and rachis sometimes broader and darker, those of the segments adaxially narrower, commonly whitish, abundant, but not concealing the segment surface; pinnae or segments (12) 15-36 pairs, linear or narrow-oblong, spreading or slightly ascending, acute or subacute, joined by a broadly rounded sinus, or some proximal ones free, equally dilated at base or, more commonly, the acroscopic side strongly dilated and the basisopic side scarcely so, the margins entire, sometimes strongly inflexed; veins obscured by the dense scales and opaque tissue, forming a single series of areoles on each side of the costa, each areole with a free, included, excurrent veinlet, veins otherwise free toward the segment margin; sori borne near tips of included veinlets in a single, usually in-framedial, series on each side of the costa, but at maturity often so large as to touch both costa and segment margin.

This and the Mexican *P. pyrrholepis* (Fée) Maxon are hardly distinct, the latter perhaps differing only in its much narrower rhizome (and somewhat narrower laminar) scales.

Polypodium sanctae-rosae (Maxon) C. Chr. Index Fil. Suppl. 62. 1913. *Goniophlebium sanctae-rosae* Maxon, Contr. U.S. Natl. Herb. 13: 8. 1909 (type from rocks and trunks of oaks near Santa Rosa, Baja Verapaz, *Tuerckheim II-1607*).

In forests or wooded ravines, rarely in open fields, on tree trunks or on rocks or rocky slopes, 1,100-2,200 m.; Baja Verapaz; Chiquimula; Guatemala; Huehuetenango; Jalapa; Quezaltenango; El Quiché; San

Marcos; Santa Rosa; Zacapa. Mexico; Honduras; El Salvador; Nicaragua.

Plants epiphytic, epipetric, or rarely terrestrial; rhizome long-creeping, 3.5-6 mm. thick, completely obscured by scales, these 0.4-1 mm. long, and often nearly as broad, circular or circular-ovate, most of them tightly appressed and imbricate, bicolorous, black or blackish, with a very narrow, brown to tawny, fimbriate margin; leaves 24-75 cm. long, 6-14 cm. broad, petiolate; petiole 7-30 cm. long, somewhat shorter than the lamina, yellowish to reddish brown, usually covered completely with scales similar to those of the rhizome, but larger (to 2 mm.) and often with long-ciliate margins and hairlike tips; lamina deeply pinnatisect, or fully pinnate toward the base, subdeltoid or deltoid-oblong, abruptly reduced to a subconform, adnate apical segment, not or scarcely reduced at base, chartaceous or subcoriaceous, both surfaces copiously scaly, often so densely abaxially as to fully obscure the tissue, the scales 1-5 mm. long, linear-lanceolate to filiform, from an abruptly dilated base, setose or ciliate, whitish to orange, but with a castaneous or blackish dot at point of attachment; rachis copiously scaly as on the segments, but the scales sometimes broader and almost completely black or castaneous; pinnae (segments) 15-36 pairs, linear-deltoid, spreading or slightly ascending, acute, joined by a subacute to broadly rounded sinus, or some proximal ones free, most of them rather equally dilated on both sides at base, the margins entire, sometimes strongly inflexed; veins obscured by the dense scales and opaque tissue, forming a single series of areoles on each side of the costa, each areole with a free, included, excurrent veinlet, veins otherwise free toward the segment margin; sori slightly impressed, borne near the tips of included veinlets in a single series, inframedial, between costa and segment margin.

***Polypodium sororium* H. & B. ex Willd. in L. Sp. Pl. 5: 191. 1810.**

Apparently represented in Guatemala by a single collection: *Tuerckheim II-488*, ed. Donn.-Sm. 8354, on tree trunk in forest, 350 m., Cubilguitz, Alta Verapaz; elsewhere, on mossy rocks or tree trunks, in forests at low elevations (sea level to 800 m.); West Indies; southern Mexico; Honduras; Nicaragua; Costa Rica; Panama; Colombia; Venezuela.

Plants epiphytic or terrestrial; rhizome creeping, densely scaly, the scales 2-5 mm. long, appressed to spreading, deep orange, narrow-deltoid, the margins entire, basifixed, not or scarcely pubescent at the base; leaves approximate to subdistant, 25-75 cm. long, 10-25 cm. broad, petiolate; petiole 10-25 cm. long, yellowish to reddish brown, puberulent or glabrescent; lamina pinnate, ovate or deltoid-ovate, tapering gradually or somewhat abruptly to a pinnatifid apex, scarcely reduced at base, the tissue papyraceous, somewhat pubescent on costae (and often the veins) on both sides, and remotely ciliate on the pinna margins, the tissue between the veins glabrous (or pubescent on young plants); rachis yellowish to reddish brown, sparsely pubescent abaxially, rather densely so adaxially; pinnae 10-20 (24) pairs, approximate to well-spaced, free, or the distal ones joined by a narrow wing (the sinuses very broadly rounded), lanceolate or elliptic-lanceolate, acute to attenuate, most of them abruptly constricted at base, but there broadly adnate on both sides (or sometimes obliquely angled basiscopically), the margins essentially entire, sometimes weakly sinuate, the proximal pinnae scarcely reduced; veins free; sori round, or more commonly somewhat elongated, in a single,

medial to slightly inframedial line between costa and pinna margin; sporangia essentially naked.

This does not differ markedly from *P. rhachipterygium*, and the latter might be better considered a variety of *P. sororium*. *Polypodium rhachipterygium* has generally broader laminae, with segments all, or mostly all, joined at the rachis by a narrow wing, with pubescence confined to the adaxial side of axes, and the veins frequently merging to form a nearly uninterrupted line of costal areoles. But these are purely quantitative differences in what may be merely a quite variable species.

The plants here recognized as *P. sororium* traditionally have been named *P. dissimile* L., but it has been found that the latter name must be applied to the species commonly known as *P. chnoodes* Spreng. For a full explanation of this confusing matter, see discussion under the treatment of *P. dissimile*.

Polypodium subpetiolatum Hook. in Benth. Pl. Hartweg. 54. 1840. *P. biserratum* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 38, t. 9, f. 1. 1842.

In forests or on open slopes, on tree trunks, logs, rocks, or rocky ground, 1,800-2,800 m.; Escuintla; Guatemala; El Progreso. Mexico.

Plants epiphytic or epipetric, rarely terrestrial; rhizome creeping, densely scaly, the scales 3-6 mm. long, tawny to orange or brown, appressed to spreading, broad and amorphous to ovate-acuminate, or narrowly deltoid and attenuate at the petiole base, often comose at point of attachment with some filiform, castaneous trichomes, the margins entire or minutely and remotely denticulate; leaves approximate to subdistant, 20-80 cm. long, 9-24 cm. broad, petiolate; petiole 10-20 cm. long, stramineous to grayish or greenish brown, essentially glabrous; lamina pinnate, oblong-deltoid, terminating rather abruptly in a pinnatifid apex, not or scarcely reduced at base, the tissue firm-herbaceous to chartaceous, whitish-pubescent on the costae and (usually) the veins on both sides, and often somewhat ciliate along the pinna margins (but leaf tissue between veins otherwise glabrous); rachis yellowish, glabrous or sparsely pubescent; pinnae 10-25 pairs, approximate to somewhat spaced, alternate, lanceolate or oblong-lanceolate, acute or subacute, margins biserrate to crenate-serrate, broadly rounded to truncate at base (usually more obliquely so basiscopically), distal ones adnate, the rest sessile or subsessile and essentially free; veins 3- to 4-forked, free, or often some of the branches merging to form costal areoles; sori round, in a single, inframedial line between costa and pinna margin; sporangia naked or sparsely and minutely glandular-setulose.

Numerous specimens have been misdetermined at *P. subpetiolatum* in various herbaria, but the species is far less common than one would suspect. Maxon's study [Contr. U.S. Natl. Herb. 8(3) 1903] pointed out many of the errors in identification of species within this complex. Thus circumscribed, *P. subpetiolatum* apparently is not to be expected outside of Mexico and Guatemala.

Polypodium thyssanolepis A. Br. ex Kl. *Linnaea* 20: 392. 1847. *Goniophlebium thyssanolepis* (A. Br. ex Kl.) Moore, *Index Fil.* 396. 1862. *P. purpusii* Christ, *Bull. Herb. Boissier* II. 7: 416. 1907.

In forests, thickets, wooded ravines, or open slopes, on rocks or rock outcrops on cliffs, occasionally in soil of rocky slopes, 1,000-2,500 m.; Baja Verapaz; Chiquimula; Huehuetenango; Quezaltanango; Sololá; Zacapa. Southwestern United States (Arizona, Texas); Greater Antilles; Mexico; Honduras; Nicaragua; Costa Rica; Panama; Colombia; Venezuela; Ecuador; Peru; Bolivia.

Plants epipetric, or occasionally terrestrial; rhizome creeping, 1.5-4 mm. thick, often entangled with brown-tomentose roots, and densely scaly, the scales 1-4 mm. long, 0.2-0.6 mm. broad, lanceolate or ovate-lanceolate, acute or acuminate, appressed, bicolorous, orange to brown with broad, blackish centers, the margins erose or erose-fimbriate; leaves well-spaced to crowded or subfasciculate, 10-58 cm. long, 3-10 cm. broad, long-petiolate; petiole 6-32 cm. long, commonly longer than the lamina, yellowish to reddish brown, often completely covered with scales, these 0.6-1.2 mm. long and often nearly as broad, circular to broadly ovate, tawny or whitish, with a roundish, castaneous to blackish center, the margins erose-fimbriate; lamina deeply pinnatisect, or rarely pinnate at base, deltoid or deltoid-oblong, abruptly reduced to a subconform, adnate, apical segment, not reduced at base, chartaceous to subcoriaceous, rachis and abaxial surface copiously scaly, with scales similar to those of the petiole, adaxial surface rather sparsely scaly, the scales to 1 mm. long, whitish, filiform, from an abruptly dilated, often stellate base; segments 3-12 (15) pairs, broadly elliptic to elliptic-lanceolate, spreading or slightly ascending, obtuse to subacute, joined by a broadly rounded sinus, strongly and subequally dilated at base on both sides, the margins entire, occasionally strongly inflexed; veins obscured by the dense scales and opaque tissue, forming a series of costal areoles, each with a free, included, excurrent veinlet, thereafter free toward the margin; sori superficial, borne in the areoles in a single series on each side of the costa, medial, but often appearing supramedial because of the strongly inflexed segment margin.

Polypodium triseriale Sw. *J. Bot. (Schrader)* 1800 (2): 26. 1801. *P. brasiliense* Poir. in *Lam. Encycl. Meth. Bot.* 5: 525. 1804. *Goniophlebium triseriale* (Sw.) Pich.-Serm. *Webbia* 31: 248. 1977.

In forests, thickets, and wooded ravines, on tree trunks, or on mossy rocks or rocky slopes, 50-1,600 m.; Alta Verapaz; Chiquimula; Izabal; Petén; San Marcos; Santa Rosa; Sololá; Suchitepéquez; Zacapa. Florida; West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Plants terrestrial, epipetric, or, more commonly, epiphytic; rhizome long-creeping, 0.4-1.2 cm. thick, amply to densely scaly, the scales 3-6 mm. long, ovate-acuminate to linear-attenuate, somewhat appressed at base, but spreading at the tips, dark brown to blackish or with a narrow, lighter brown margin, minutely clathrate, the margins subentire or somewhat erose; leaves approximate to widely spaced, 35-100 cm. long, 21-45 cm. broad, petiolate; petiole 12-35 cm. long, stramineous to reddish brown, glabrous; lamina

pinnate, deltoid or deltoid-oblong, scarcely or not reduced at base, terminating in a conform, often short-stalked, apical segment, firm-herbaceous to chartaceous, essentially glabrous, but rachis and costae occasionally with a few, scattered, minute, dark, filiform scales abaxially; pinnae 4-10 pairs, larger ones 15-28 cm. long, 2-4 cm. broad, widely spaced, sessile, or proximal ones very short-stalked, lanceolate, obtuse to acute or attenuate, cuneate at base, a few subapical pairs broadly adnate, the margins subentire, not or slightly cartilaginous; venation regularly areolate, all veins distinct and commonly prominulous, primary ones spreading from the costa at a 40-50° angle, straight to somewhat flexuous, secondary (connecting) veins obliquely arching and joining adjacent primary veins to form a series of 3-6 areoles between costa and pinna margin, these very similar in size and shape and each containing a single, free, excurrent veinlet; sori round, borne on tips of free veinlets, commonly (1) 2- (3) seriate between costa and margin; sporangia glabrous.

This and *P. fraxinifolium* are very similar. See treatment of the latter for further discussion.

EXCLUDED SPECIES

Polypodium fructuosum Maxon & Weath. ex Weath. Contr. Gray Herb. 65: 12. 1922.

Polypodium fructuosum apparently is known only from Nicaragua, Costa Rica, and Panama, although Seymour (Phytologia 31: 166. 1975) cited an undesignated Guatemalan collection at Pringle Herbarium (VT). At my request, David Barrington, curator of the herbarium, searched for the specimen, but was unable to locate it. *Polypodium fructuosum* is perhaps most closely related to *P. lanceolatum* (subg. *Pleopeltis*), but is distinguished from the latter by its clathrate scales with large, clear lumina and thin cell walls, and by the fertile leaves which are so strongly constricted that the large sori typically project beyond the lamina margin. Leaves of *P. lanceolatum* are scarcely or not at all dimorphous, and rhizome scales are not or only somewhat clathrate.

POLYSTICHUM Roth

Plants terrestrial; rhizome commonly stout, erect or suberect, amply scaly; leaves monomorphic, long-petiolate, fasciculate; petiole not articulate, scaly (especially at base), abaxially rounded, adaxially sulcate; lamina simply pinnate to decompose (or rarely simple), the major axes sparsely to densely scaly, firm-herbaceous to (more often) coriaceous, lanceolate, elliptic, or broadly ovate, tapering to a pinnatifid apex, some species with a proliferous bud borne on the rachis near the apex; rachis narrowly sulcate adaxially, with the raised, parallel ridges continuous (sometimes inconspicuously) as ridges on the costae, scaly, the scales often twisted and hairlike; pinnae few to (more commonly) many, spreading to strongly ascending; pinnules (or pinnae on simply pinnate

species) spinulose, especially on the apex and acroscopic margin, anadromous, commonly inequilateral at base, basiscopically cuneate, acroscopically truncate and more strongly produced and often with a conspicuous auricle; venation anadromous, veins free, usually forked and reaching the margin; sori abaxial on the veins, commonly borne on the vein branches; indusium minute to conspicuous, peltate, persistent, fugacious or (in a few species) lacking; paraphyses lacking; sporangium long-stalked; spores monolete, bilateral, with perine.

The genus is cosmopolitan, with approximately 150 species occurring in temperate and tropical regions in both the New and the Old World. However, the total number of species is highly questionable, as monographic work has been practically nonexistent. *Polystichum*, while readily distinguishable at the generic level (at least in Central America), has a more confusing array of components than perhaps any other genus of ferns. Even the most diagnostic morphological features—scales, indusia, leaf texture, dissection of segments—sometimes seem to blend insensibly from one specimen to the next. In any given geographic area, there appear (at least superficially) to be a number of rather recognizable taxa. However, while working with large collections in such areas, one can find quantities of specimens which are intermediate between each. The situation, then, hints very strongly at widespread hybridization and even backcrossing. Some European and North American workers have pointed out such problems in their areas of interest (*e.g.*, see Wagner, Amer. Fern J. 63: 99. 1973), so the monographer who plans to study the tropical species must be prepared to face the same dilemma.

The following treatment is hardly definitive. Among hundreds of specimens I have examined from Guatemala and adjacent areas, there are far too many which I have been obliged to annotate in a tentative manner. The key to Guatemalan species will function effectively only on those specimens whose features do not vary too widely from the "recognizable taxa" mentioned above. There have been no provisions made for the large array of intermediates, for to do this would have necessitated the naming of a multitude of varieties and forms, all of which is meaningless pending complete monographic and field studies which include the problems of hybridization. Previous lack of understanding of taxa has already resulted in too many names and too much confusion.

Species of *Polystichum* in Guatemala may be generally recognized as deep forest plants occurring at middle to upper elevations, with stout, erect rhizomes, decompound, coarse-textured laminae, spinulose ultimate segments, and peltate (when present) indusia.

- a. Lamina rarely over 5 cm. broad, pinnate, or if 2-pinnate the pinnules 2-7 pairs.
 - b. Lamina pinnate; sori indusiate (but sometimes fugacious). *P. munchii*.
 - b. Lamina 2-pinnate; sori exindusiate. *P. polyphyllum*.
- a. Lamina of mature leaves (7) 9-35 cm. broad, 2-pinnate, the pinnules (8) 12-30 pairs (or more).
 - c. Rachis bearing a proliferous bud near the apex; sori exindusiate. *P. platyphyllum*.
 - c. Rachis lacking a proliferous bud; sori indusiate, but indusia sometimes minute and fugacious (exindusiate in *P. mickelii*).
 - d. Scales of petiole and rachis conspicuously spinulose (the teeth to 0.4 mm. long), very densely covering, and often nearly obscuring, the axes. *P. furfuraceum*.
 - d. Scales of petiole and rachis entire (or minutely and inconspicuously dentate or ciliate), sparse to abundant.
 - e. Mature indusia deep reddish brown; largest pinnae (15) 17-25 cm. long; pinnules scarcely or not at all incised, the basal auricle raised but not often discrete. *P. erythrosorum*.
 - e. Mature indusia whitish to tawny or medium brown, or lacking; largest pinnae 5-16 (19) cm. long.
 - f. Sori exindusiate; petiole scales orange to light brown, thin, broadly ovate, larger ones 4-6 mm. broad. *P. mickelii*.
 - f. Sori indusiate (although indusia sometimes fugacious).
 - g. Lamina broadest near the middle; 8-15 proximal pairs of pinnae gradually reduced; basal pair of pinnae $\frac{1}{4}$ - $\frac{3}{4}$ as long as the largest middle ones.
 - h. Scales of rhizome and petiole base lustrous, blackish, concolorous or with a thin brown margin; rachis scales deep orange, often mixed with some lustrous, blackish ones; free pinnae 25-32 (35) pairs. *P. distans*.
 - h. Scales of rhizome and petiole base whitish to tawny, strongly bicolorous; rachis scales whitish to tawny (blackish ones lacking); free pinnae 32-42 pairs. *P. ordinatum*.
 - g. Lamina broadest toward the base, 1-4 proximal pairs of pinnae slightly reduced; basal pair of pinnae more than $\frac{3}{4}$ the length of the larger ones.
 - i. Scales of petiole base mostly appressed to ascending, thick and rigid, often convexo-concave; rachis scales deep orange to reddish brown; largest pinnae (on mature leaves) 15-19 cm. long. *P. hartwegii*.
 - i. Scales of petiole base spreading, thin and flat; rachis scales bright or pale orange; pinnae commonly less than 15 cm. long.
 - j. Scales of petiole base 6-12 mm. long, 1-2 mm. broad; free pinnae commonly 16-22 pairs; pinnules approximate to subdistant. *P. fournieri*.
 - j. Scales of petiole base 15-25 mm. long, larger ones 3-6 mm. broad; free pinnae commonly 22-30 pairs; pinnules mostly crowded to imbricate.
 - k. Mature indusia 0.8-1.5 mm. broad; pinnules subentire to crenulate, slightly to moderately spiny (more strongly so on auricle and apex); basal pinnules scarcely or moderately incised, the auricle rarely nearly free. *P. rachlichlaena*.
 - k. Mature indusia 0.6 mm. broad or less; pinnules crenate to deeply lobed, moderately to strongly spiny; basal (and often other) pin-

nules commonly cut deeply to costule, the auricle thus nearly free. *P. muricatum*.

Polystichum distans Fourn. Mex. Pl. 1: 91. 1872. *P. pallidum* Fourn. loc. cit. (not Gardn. 1842 nor Todaro, 1866) (type from Oaxaca, Mexico, *Ghiesbreght s.n.*).

In wet forests, thickets, and wooded ravines, often along streams or at the bases of waterfalls, 2,000-3,200 m.; Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Santa Rosa; Sololá. Southern Mexico (type from Orizaba, Veracruz, *Schaffner 217a*); El Salvador; Costa Rica?

Plants terrestrial; rhizome stout, erect, amply provided with linear or filiform, lustrous, dark-brown to blackish, usually bicolorous scales; leaves 40-90 cm. long, 9-18 cm. broad; petiole 12-27 (30) cm. long, yellowish to light brown, scaly (often densely so, especially at base), the scales thin, flat, mostly spreading, commonly lustrous and blackish, often with a dark-brown margin, these ovate to lanceolate, 1-2.5 cm. long and 0.15-0.25 (0.3) cm. broad; lamina bipinnate, chartaceous to subcoriaceous, lanceolate-elliptic, gradually and obviously reduced toward the base, broadest near the middle; rachis lacking a proliferous bud, amply to abundantly scaly, the scales linear-lanceolate to twisted-filiform, deep orange, a few or many blackish or with blackish centers, the margins entire; pinnae 25-32 (35) free pairs, the largest 5-12 cm. long and 1.2-2.2 cm. broad, sessile, subdistant proximally to crowded distally, spreading to ascending, 8-14 proximal pairs reduced, basal ones scarcely to strongly deflexed, $\frac{1}{2}$ - $\frac{3}{4}$ as long as the larger central ones; pinnules (12) 16-24 free pairs (on largest pinnae), approximate to crowded, subsessile, acropically truncate and auriculate (at least the basal pinnules usually deeply incised at the auricle) scarcely to moderately spinulose, the margin subentire to crenate, and plane to strongly revolute; veins distinct or indistinct, mostly 1- to 2-forked; sori medial to inframedial, essentially uniseriate, commonly confluent at maturity; mature indusia tawny or light brown, fugacious to subpersistent, 0.3-1 (1.3) mm. broad.

I must admit to some confusion in applying the name *P. distans* to the plants included in the above description. I have not seen the type collection and am uncertain if this is distinct from *P. pallidum*. In Fournier's original descriptions he describes some of the scales of the latter as "medio nigrescentibus margine ferrugineis" and those of *P. distans* "subfuscis, medio obscurius coloratis." Many collections in herbaria with lustrous, black scales on the petiole base have been determined as *P. distans*. I have examined the holotype (P) of *P. pallidum*, and although it lacks a rhizome and petiole base, numerous rachis scales are lustrous black with very narrow brownish margins, so I presume the scales of the missing petiole base would be similar. Other specimens I have seen, which match the type in every other way, have lustrous black scales on rhizome and petiole base, and I take this to be an important diagnostic character. Other differences in the

two species noted by Fournier deal with position of sori and relative persistence of indusia and crowding of pinnae and pinnules, none of which are very strong or consistent characters.

Photos (Morton, U.S. National Herbarium) of syntypes of "*P. distans* var. β Fournier" (*Bourgeau 2350-bis & 3189*) show plants with the aspect of *P. pallidum*, except that pinnae are somewhat longer and most pinnules more deeply incised. Morton's photo label describes *Bourgeau 3189* as having "indusia dark brown, deciduous," although the original description of typical *P. distans* describes them as persistent. All of this merely adds to the confusion, but it is my guess that there are a small number of Southern Mexican and Guatemalan specimens which are perhaps the true *P. pallidum* of Fournier, and that there are also two other forms or varieties; one, very common, in Mexico and Guatemala, which has more rigid and coriaceous, strongly ascending pinnae (corresponding to *P. distans*); the other, made up of scattered specimens from Guatemala to Costa Rica, which are larger and more dissected.

For the purposes of this treatment, I choose to recognize *P. distans* as described above, placing *P. pallidum* in synonymy. The small number of Guatemalan specimens which have larger laminae and more deeply lobed pinnules I have annotated in various herbaria as "*P. distans vel aff.*" These may or may not merit distinction, but I take them to be comparable to Fournier's improperly named and described "var. β ."

I would have rather used the name *P. pallidum*, placing *P. distans* in synonymy, for the type of the latter appears unavailable, and the type of the former *has* been examined and is closely matched by a number of collections. Unfortunately the name is a later homonym, and since the taxonomic problems are still unresolved, there seems no need to add further nomenclatural confusion.

Polystichum erythrosorum A. R. Smith, Proc. Calif. Acad. Sci. Ser. IV. 40: 225. 1975.

On the forest floor, in high montane forests, 2,500-3,000 m.; Huehuetenango; El Progreso; San Marcos; Totonicapán? Southern Mexico (type from Municipio Motozintla de Mendoza, Chiapas, 3,000 m., *Breedlove & Smith 22709*).

Rhizome stout, short, erect, densely covered with ovate to lanceolate, rigid scales, near the petiole base these to 1.5 cm. long and 0.5 cm. broad, lustrous, deep brown (some nearly blackish), stout, often convexoconcave; leaves to 1 m. long and 0.4 m. broad; petiole to 50 cm. long and 0.8 cm. in diameter, light to yellowish brown (darker at base),



FIG. 67. *Polystichum*. a-b, *P. fournieri*: a, habit, $\times \frac{1}{2}$; b, pinna base with scales and sori, $\times 6$; c, *P. rachichlaena*, pinna base with scales and sori, $\times 6$; d, *P. platyphyllum*, lamina (adaxial side) near apex, showing configuration of rachis and proliferous bud, $\times 3$; e, *P. furfuraceum*, petiole scale, $\times 6$; f, *P. ordinatum*, petiole scale, $\times 6$; g, *P. distans*, petiole scale, $\times 6$; h, *P. mickelii*, petiole scale, $\times 6$.

densely scaly, the scales mostly light brown, flaccid and appressed, but also some others, less abundant, more like those of the petiole, dark brown to blackish, or bicolorous; lamina 2-pinnate, coriaceous or subcoriaceous, ovate, gradually terminating in a pinatifid apex, scarcely reduced at base; rachis lacking a proliferous bud, abundantly scaly, the scales lanceolate to filiform, deep orange or reddish brown to lustrous and blackish, the margins often minutely setulose; pinnae commonly 20-28 pairs, to 25 cm. long and 3 cm. broad, sessile, subdistant, linear-lanceolate, 2-4 proximal pairs slightly reduced, spreading to ascending, the basal pair usually deflexed, $\frac{3}{4}$ - $\frac{7}{8}$ the length of the larger central ones; pinnules to 30 pairs (on larger pinnae), not crowded, sessile or subsessile, inequilateral at base, basiscopically cuneate, acroscopically truncate and auriculate (the auricle rarely incised), spinulose at the apex and on the auricle but rarely along the margin, the margin subentire to crenulate or serrulate, slightly revolute; veins 1- to 3-forked, indistinct to obscure, often provided with orange, fibrillose scales abaxially; sori medial to inframedial, uniseriate (except near the base), subdistant, not or scarcely confluent at maturity; mature indusia dark reddish brown, subpersistent, 0.6-0.8 mm. broad.

Polystichum fournieri A. R. Smith, Amer. Fern J. 70: 27. 1980 (*nom. nov.* for *P. muelleri* Fourn. Mex. Pl. 1: 91. 1872) (not Schum. 1803).

On slopes, ridges, or ravines, in wet, montane forests, 1,800-2,900 m.; Chimaltenango; Escuintla; Jalapa; El Progreso; El Quiché; Sacatepéquez; San Marcos; Sololá. Southern Mexico (syntype from Mexico "in pinetis prov. Chiapas," *Linden s.n.*; designated the lectotype by Alan R. Smith); Honduras; El Salvador; Costa Rica.

Plants terrestrial; rhizome stout, erect, amply provided with orange or dark-brown, linear or linear-lanceolate scales; leaves 0.5-1.2 m. long, 0.1-0.2 m. broad; petiole to 60 cm. long, stramineous to dark brown, commonly much darker at base, sparsely scaly, but the basal scales more abundant, thin, flat, mostly spreading, tawny to dark brown, concolorous to bicolorous, lanceolate, 0.6-1.2 cm. long, 0.1-0.2 cm. broad; lamina 2-pinnate, chartaceous, narrow-ovate to lanceolate, broadest near the base; rachis lacking a proliferous bud, sparsely scaly, the scales orange (often pale), a few or many of them with margins minutely setulose; pinnae 16-22 free pairs, the largest 5-12 cm. long and 1.5-2.2 cm. broad, sessile, approximate to crowded, spreading to slightly ascending, 1-3 (5) proximal pairs slightly reduced, the basal ones often deflexed and $\frac{4}{5}$ to nearly as long as the largest central ones; pinnules 8-17 (19) free pairs on largest pinnae, approximate to (more commonly) subdistant, subsessile, acroscopically truncate and auriculate (the larger pinnules commonly deeply incised at base and thus the auricle often nearly free), conspicuously spinulose, the margin beyond the auricle crenate to deeply lobed, essentially plane; veins usually distinct, 1- to 2-forked; sori inframedial, discrete, or often confluent at maturity; mature indusia tawny or whitish (sometimes light brown), subpersistent, the larger ones 1-1.5 mm. broad.

This is most easily confused with *P. hartwegii*. Besides the differences noted in the key, however, there are other useful characters which may be of help in distinguishing the two. *Polystichum fournieri* is usually a much smaller species, with pinnae 5-12 cm. long, the largest ones bearing 8-17 (19) pairs of free pinnules. The larger pinnae

of *P. hartwegii* are commonly 15-19 cm. long and have 21-28 pairs of free pinnules.

Polystichum furfuraceum A. R. Smith, Proc. Calif. Acad. Sci. Ser. IV. 40: 226. 1975.

Apparently known in Guatemala from a single collection (bosque nebuloso de María Tecun, Totonicapán, alt. 3,800 m., *Molina 15888*). Southern Mexico (type from Zontehuitz, Chiapas, *Münch 113.*).

Plants terrestrial; rhizome unknown; leaves coarse, rigid, to 1 m. long and 0.3 m. broad; petiole to 30 cm. long and 0.7 cm. in diameter, much shorter than the lamina, stramineous to light brown, often completely obscured by ovate, dark- or rusty-brown scales, these to 1.8 cm. long and 1 cm. broad, attenuate, with the margin densely and conspicuously setose; lamina 2-pinnate, coriaceous or subcoriaceous, deltoid-lanceolate, gradually terminating in a pinnatifid apex, scarcely or not at all reduced at base, abundantly scaly (especially on the abaxial side); rachis stramineous to light brown, densely scaly as on the petiole, lacking a proliferous bud; pinnae numerous, sessile or subsessile, approximate to imbricate, spreading to ascending, or a few proximal ones deflexed, linear, acute, pinnate; pinnules 30-45 pairs (on larger pinnae), mostly short-stalked, inequilateral at base, basiscopically cuneate, acroscopically auriculate and truncate, spinulose at apex and on the auricle, and often along the margin, the margins somewhat revolute; veins 1-forked (or 2- to 3-forked in the auricle), indistinct to obscure; sori medial to inframedial, uniseriate, sometimes confluent at maturity; indusia tawny to light brown, peltate, subpersistent, or falling away at maturity.

Polystichum hartwegii (Kl.) Hieron. (as "*hartwigii*") *Hedwigia* 46: 355. 1907. *Aspidium hartwegii* Kl. *Linnaea* 20: 366. 1847 (type "in montibus Las Nubes prope urbem Guatemala," *Hartweg 631*). *Polystichum grande* Fée, *Mém. Fam. Foug.* 8: 98. 1857.

In wet forests, on slopes, or in wooded ravines, frequently on stream banks, 1,250-2,850 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Jalapa; Quezaltenango; El Quiché; San Marcos; Santa Rosa; Sololá; Suchitepéquez; Totonicapán; Zacapa. Southern Mexico to Nicaragua; Costa Rica?

Plants terrestrial; rhizome stout, erect, amply provided with light- to dark-brown, linear or linear-lanceolate scales; leaves to 1.5 m. long, 17-35 cm. broad; petiole 35-65 cm. long, light brown to yellowish, sparsely scaly, but ample at base, the basal scales rather rigid and thick, appressed to ascending, most of them convexoconcave, dark reddish or grayish brown, concolorous or somewhat bicolorous, lanceolate or linear-lanceolate, 1-1.5 (2) cm. long, 0.1-0.3 cm. broad; lamina 2-pinnate, chartaceous, narrow-ovate to lanceolate, broadest toward the base; rachis lacking a proliferous bud, scaly (sometimes sparsely so), the scales mostly deep orange or reddish brown, their margins essentially entire; pinnae (18) 22-30 free pairs, the largest 15-22 cm. long and 2.5-3 cm. broad, sessile, approximate to crowded, ascending, 1-4 (5) proximal pairs slightly reduced, the basal ones often deflexed, these commonly more than $\frac{1}{4}$ the length of the largest central ones; pinnules 21-30 free pairs (on largest pinnae), approximate to crowded, subsessile, acroscopically truncate and auriculate (the largest pinnules commonly deeply incised at

base and often nearly free), moderately to strongly spinulose, the margin beyond the auricle crenate to deeply lobed, essentially plane; veins usually distinct, 1- to 2-forked; sori mostly inframedial, discrete, or often confluent at maturity; mature indusia tawny, subsistent, the larger ones 0.5-1.2 mm. broad.

This and *P.ournieri* can be easily confused. See treatment of the latter for a more detailed comparison of characters.

I have examined a number of Guatemalan specimens which at first appear to be *P. hartwegii*, but on which the scales of the petiole base are flat and blackish, as in *P. distans*. Most have the long pinnae and more highly dissected pinnules of the former, and a few have the thicker textured and somewhat revolute pinnule margins of the latter. Some are sterile, some are fertile. Few appear to have abortive spores or sporangia. In short, these collections have so many mixed characteristics that they neither match the recognized species nor constitute a third, distinct taxon. It may be that this group of specimens affords some evidence of backcrossing; however, this question lies beyond the scope of the present treatment.

Polystichum mickelii A. R. Smith, Amer. Fern J. 70: 27. 1980.

On the forest floor, in mountain forests, 1,300-2,400 m. Alta Verapaz; Sacatepéquez; San Marcos. Southern Mexico (type from Cerro Zempoaltepetl, Oaxaca, *Mickel & Leonard 4836*); Honduras.

Plants terrestrial; rhizome not seen (but evidently stout, erect, scaly); leaves to over 1 m. long and 0.3 m. broad; petiole 30-50 cm. long, often nearly the length of the lamina, 3-6 mm. in diameter, stramineous to light brown (darker at base), sparsely scaly, except near the base more amply provided with broad, ovate, attenuate, orange to light-brown scales, these to 2 cm. long and 0.6 cm. broad, rather thin and flaccid, sometimes bicolorous, with a thin, dark-brown, median stripe, entire to faintly erose; lamina 2-pinnate, chartaceous to subcoriaceous, ovate-attenuate, gradually terminating in a pinnatifid apex, scarcely or not at all reduced at base, sparsely scaly; rachis lacking a proliferous bud, narrowly and deeply furrowed adaxially, stramineous, sparsely provided with linear or filiform, orange or light-brown scales, larger ones often with minutely setulose margins; pinnae 20-24 pairs, to 18 cm. long and 3 cm. broad, subsessile to short-stalked, subdistant, spreading to ascending, or the basal pair deflexed, linear-lanceolate, attenuate; pinnules 20-24 pairs (on larger pinnae), subsessile or short-stalked, inequilateral at base, basiscopically cuneate, acropically truncate and auriculate (the auricle raised but rarely discrete), spinulose at apex and on the auricle, the margins subentire to dentate, slightly revolute; veins 1-forked (or more in the auricle), indistinct to obscure; sori exindusiate, medial to inframedial, uniseriate (except near the base), subdistant, not confluent at maturity.

Several collections from Quezaltenango (*Steyermark 33834, 34367, 35194*, alt. 1,350-1,500 m.) are very similar to *P. mickelii*, in size, shape, texture, and especially in the very large petiole scales. However, all have very small, inconspicuous indusia. Alan Smith informs

me (*in litt.*) that these match some *Purpus* collections he has seen from Chiapas, which are also indusiate. He also points out that in the Steyermark and *Purpus* collections "the rachis scales are also different, some broader, ovate-lanceolate and decidedly erose-denticulate at margin (all filiform or linear and entire in *P. mickelii*)."

Polystichum munchii (Christ) C. Chr. Index Fil. 585. 1906. *Aspidium munchii* Christ, Bull. Herb. Boissier II. 1: 1120. 1901 (type from Chiapas, Mexico, *Münch 24*).

Known in Guatemala only from one collection, *Tuerckheim* (ed. Donn.-Sm. 851) " 'In Feldsspalten bei Coban 4500,' Alta Verapaz." The only other collections known thus far are the type, and *Münch 14*, also from Chiapas.

Plants epipetric (perhaps also terrestrial); rhizome stout, erect or ascending, densely scaly, the scales 3-8 mm. long, 0.5-1 mm. broad, linear to lanceolate, entire, narrowly acute, dull brown or black and lustrous, with a narrow, dull-brown margin; leaves erect, rigid, fasciculate, 20-45 cm. long, 3-5 cm. broad; petiole 3-14 cm. long, commonly much shorter than the lamina, stramineous to light brown, sparsely to amply provided with orange to light-brown scales, these linear, often filiform and tortuous, but usually broader at the petiole base; lamina pinnate, chartaceous or subcoriaceous, linear-lanceolate, tapering gradually to a pinnatifid apex, usually not greatly reduced at base; rachis stramineous or light brown, sparsely provided with orange or light-brown filiform scales, lacking a proliferous bud; pinnae 10-22 pairs, most of them subdistant, patent or slightly ascending, 1.5-2.5 cm. long, 0.8-1.5 cm. broad, mostly stalked, ovate to subdeltoïd, inequilateral at base, acute and often spinulose at apex, the margin crenulate or broadly dentate, rarely spinulose, except commonly so at the tip of the basal acroscopic auricle, essentially glabrous, or a few filiform scales along the stalks; veins obscure, 2- to 3-forked; sori uniseriate (sometimes biseriate at pinna base), medial to supramedial; indusia dark brown, peltate, subpersistent, or falling away at maturity.

Although hardly confused with any Guatemalan species, this is very similar to *P. triangulum* (L.) Fée of Hispaniola and *P. echinatum* (Gmel.) C. Chr. of the Greater Antilles, and eventually all three may be considered conspecific. *Polystichum triangulum* differs perhaps only in the densely packed and broader scales of the rachis. *Polystichum echinatum* is presumed to differ in that the lamina is more strongly reduced at base and the pinnae are generally narrower, more numerous, and more regularly spinulose. However, I have seen a number of specimens of *P. echinatum* from the Greater Antilles, notably *Maxon & Killip 998* (Jamaica) and *Pollard & Palmer 143* (Cuba) which have fewer, broader, scarcely spinulose pinnae, and laminae somewhat to obviously reduced at base.

Polystichum muricatum (L.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 278. 1852. *Polypodium muricatum* L. Sp. Pl. 1093. 1753.

Apparently represented in Guatemala by a single collection (Santa María de Jesus, Quezaltenango, 1,530 m., *Steiermark 34367*); elsewhere, on slopes and ridges in wet, montane forests, 1,200-2,100 m. Southern Mexico; Honduras; Nicaragua; Costa Rica; Colombia; Venezuela; Peru (?).

Plants terrestrial; rhizome stout, erect, amply provided with lanceolate to linear-lanceolate, bright- or dark-brown, essentially concolorous scales; leaves to 1.5 m. long and 0.25 m. broad; petiole to 0.5 m. long, stramineous to light brown, abundantly scaly, the scales thin, flat, mostly spreading, light brown, concolorous or inconspicuously bicolorous, these broadly ovate, 1.5-2.5 cm. long, 0.3-0.6 cm. broad; lamina 2-pinnate, firm-membranaceous, ovate, broadest toward the base; rachis lacking a proliferous bud, amply to abundantly scaly, the scales linear-lanceolate to (mostly) twisted-filiform, orange, their margins entire; pinnae 22-28 free pairs, the largest 8-15 cm. long and 2-2.5 cm. broad, sessile, approximate to crowded, ascending, 1-4 proximal pairs slightly reduced, the basal ones often strongly deflexed, more than $\frac{3}{4}$ the length of the larger central ones; pinnules 13-28 free pairs (on largest pinnae), approximate to crowded, subsessile, or larger ones short-stalked, acroscopically truncate and auriculate, (the larger pinnules commonly deeply incised at base and the auricle often nearly free), moderately to strongly spinulose, the margin crenate to deeply lobed and essentially plane; veins usually distinct, 1- to 2-forked; sori medial to inframedial, essentially uniseriate, commonly discrete, rarely confluent at maturity; mature indusia tawny to dark brown, fugacious to subsistent, 0.2-0.6 mm. broad.

Although *P. muricatum* is similar to many other species in the general aspect of the lamina, it may be usually distinguished from most species by the large, spreading scales at and near the base of the petiole. These are essentially concolorous (though sometimes with some dark, median cells), dull brown, thin in texture, and often nearly as broad as long. Conversely, the indusia are among the smallest in the Central American species, and only rarely confluent. A large number of specimens seen in various herbaria have been wrongly named *P. muricatum*, for the species is far less common than has been generally reported.

Polystichum ordinatum (Kunze) Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 276. 1849. *Aspidium ordinatum* Kunze, Linnaea 18: 347. 1844 (type from unknown Mexican locality, *Leibold s.n.* [herb. Roem. Coll. no. 39]).

On the forest floor, in cloud forests, 2,600-3,000 m.; Guatemala; Huehuetenango. Southern Mexico.

Plants terrestrial; rhizome stout, erect, densely scaly, the scales mostly appressed, linear-lanceolate, stramineous to tawny, or more commonly bicolorous with a dark-brown median stripe and tawny margin; leaves to 1 m. long and 0.3 m. broad; petiole 11-30 cm. long, up to 6 mm. in diameter, much shorter than the lamina, stramineous to light brown, often obscured at base by the linear or linear-lanceolate, attenuate, strongly bicolorous scales, these spreading or ascending, 0.8-1.5 cm. long, 0.1-0.3 cm.

broad, subentire, whitish to tawny, commonly with a narrow, dark-brown, median stripe; lamina 2-pinnate to 2-pinnate-pinnatifid, chartaceous, lanceolate to narrow-elliptic or -ovate, gradually terminating in a pinnatifid apex, moderately to strongly reduced at base, broadest near the middle, abundantly scaly on the axes abaxially; rachis lacking a proliferous bud; pinnae numerous (32-42 free pairs), sessile, spreading to ascending, or some proximal ones deflexed, lanceolate or oblong-lanceolate, acute to attenuate, larger ones 10-15 cm. long, 1.6-2.6 cm. broad, the proximal 3-7 pairs 2.5-7 cm. long; pinnules 18-28 pairs (on larger pinnae), subsessile, inequilateral at base, basiscopically cuneate, acroscopically auriculate and truncate, the margin spinulose-crenate, deeply incised at the acroscopic (and rarely the basiscopic) base to form a nearly free, spinulose auricle; veins 1-forked (or 2-forked in the auricle), indistinct to obscure; sori inframedial, uniseriate, sometimes confluent at maturity; mature indusia 0.2-0.4 mm. broad, dark brown, peltate, subsistent or falling away at maturity.

Alan Smith (Univ. of California, Berkeley) has written, in his yet-unpublished manuscript on the Ferns of Chiapas, that "the name *P. ordinatum* has been too widely applied." With this I wholeheartedly agree. Dozens of neotropical collections have been so determined in various herbaria, and these bear little resemblance to the type. Only a few specimens from southern Mexico and Guatemala have conspicuously reduced lower pinnae and very pale petiole scales with a dark median band. All other collections I have examined from South and Central America and the West Indies are incorrectly named. (*Polystichum distans* has a number of reduced lower pinnae, but the petiole scales are blackish and lustrous.)

Polystichum platyphyllum (Willd.) Presl, Tent. Pterid. 84. 1836. *Aspidium platyphyllum* Willd. in L. Sp. Pl., ed. 4. 5: 255. 1810 (not Presl, 1849). [*P. polystichiforme* (Fée) Maxon, Contr. U.S. Natl. Herb. 13: 35. 1909?]

Not yet reported from Guatemala, but to be expected here, as it occurs in southern Mexico and Honduras. In forests and wooded ravines, 600-1,600 m.; southern Mexico; Honduras; Nicaragua; Costa Rica; Greater Antilles?; Colombia and Venezuela, south to Argentina and Paraguay.

Plants terrestrial; rhizome stout, erect or ascending, amply provided with tawny, dull-orange or medium-brown scales, these 5-15 mm. long, 1-2 mm. broad, ovate to lanceolate, subentire, acuminate or attenuate; leaves erect, fasciculate, 35-85 (100) cm. long, 10-22 (25) cm. broad; petiole 15-45 cm. long, shorter than the lamina, stramineous, scaly as on the rhizome, but distally the scales less abundant and becoming linear to filiform; lamina 2-pinnate, firm-membranaceous, ovate-attenuate, very gradually tapering to a pinnate, and at length pinnatifid, apex, slightly reduced at base, sparsely provided on the adaxial surface with minute, brown trichomes or hairlike scales; rachis stramineous, moderately provided with linear to filiform, light-brown scales, and bearing a proliferous bud in the axil of one of the distal pinnae; pinnae 18-24 pairs, spreading to ascending, the basal ones often reflexed and slightly reduced, short-stalked to subses-

sile, acute to attenuate, proximal ones pinnate and subdistant, distal ones undivided and crowded; pinnules 10-18 pairs (on larger pinnae of mature leaves), short-stalked to (distally) sessile, oblong- to ovate-rhomboid, basiscopically subentire and cuneate at base, acroscopically crenate-aristate and auriculate and truncate at base, obtuse to acute and often aristate at apex, scarcely or not at all revolute; veins distinct or indistinct, rarely obscure, 1- to 4-forked; sori relatively small, medial to (sometimes) inframedial, uniseriate (or rarely biseriate near segment base) between midrib and margin; indusia lacking.

With this should probably be included *P. polystichiforme* (Fée) Maxon, of the Greater Antilles, which is said to differ from *P. platyphyllum* in relative size and texture. I have not seen the type of the former, but the few Antillean collections I have seen closely match *P. platyphyllum*.

Polystichum polyphyllum (Presl) Presl, Tent. Pterid. 83. 1836. *Nephrodium polyphyllum* Presl, Rel. Haenck. 1: 37. 1825. *Polypodium rigidum* Hook. & Grev. Icon. Fil. t. 163. 1829 (not Aubl. 1775 nor Hoffm. 1795).

Although I have yet seen no specimens from Guatemala, a *Godman & Salvin* (s.n.) specimen from Volcán de Agua (Sacatepéquez?) was cited by Hemsley (Biol. Centr. Amer. 3: 668. 1882) as *Polypodium rigidum*. It may have been this collection that Alan R. Smith (Univ. of California, Berkeley) reported (*in litt.*) as having seen in the herbarium at either Kew or British Museum, and noted as being similar to Chiapas collections of *Polystichum polyphyllum*. The species should be expected in Guatemala, for it occurs in Chiapas, Costa Rica, Colombia, Ecuador, Peru, and Bolivia, in high montane meadows or slopes, often among rocks, or in crevices of cliffs, apparently between 3,200 and 4,500 m.

Plants terrestrial or epipetric; rhizome stout, erect, densely provided with dark-brown, ovate or lance-ovate, attenuate scales, these to 15 mm. long and 3 mm. broad, with margins sparsely ciliate; leaves erect, rigid, fasciculate, 25-45 cm. long, 2.5-4.5 (6) cm. broad; petiole (8) 12-22 cm. long, about as long as the lamina, stramineous to light brown, often somewhat muricate due to the persisting scale bases, at base densely scaly as on the rhizome, but distally the scales smaller, lighter brown, and more scattered; lamina 2-pinnate, coriaceous or subcoriaceous, linear to lanceolate, tapering gradually to a nonconform apical segment, scarcely or not reduced at base, glabrous or essentially so adaxially, moderately scaly abaxially; rachis moderately to densely scaly, the scales dark to light brown to reddish (or whitish on some South American specimens), lacking a proliferous bud; pinnae numerous, crowded to imbricate, strongly ascending, 2-3.5 cm. long, 1-1.5 cm. broad, short-stalked, obtuse to subacute, moderately scaly abaxially, the scales lanceolate to linear, often hairlike; pinnules 2-7 pairs, short-stalked, obovate, ovate, or rhomboid, the margin crenulate-dentate, slightly spinulose, slightly to strongly revolute; veins commonly obscure and 1-forked; sori exindusiate, confluent at maturity.

There should be no confusing this with other species in Guatemala. It is quite distinctive in its ascending, imbricate pinnae and its relatively few pinnules with (usually) strongly revolute margins. In addition, it is apparently confined to very high montane situations.

However, there is a problem in separating *P. polyphyllum* from *P. pycnolepis* (Kze.) Moore, a very similar species from South America which supposedly differs in having indusiate sori and longer pinnae with more numerous pinnules. Kunze describes his species “. . . indusiis peltatis, caducis. . .” I have not seen the type, but none of the specimens determined as *P. pycnolepis* in the Field Museum herbarium have indusiate sori. (This includes a large number of sheets from both South and Central America.) Furthermore, some of these specimens of “*P. pycnolepis*” have shorter pinnae and fewer pinnules, enough so that these characters seem to blend with those of *P. polyphyllum*. Hence, a reexamination of the relationship between the two taxa is necessary.

Polypodium rigidum is included here as a synonym. The plate in the “Icones Filicum” illustrates less strongly ascending pinnae and nearly plane segment margins, but these characters in *P. polyphyllum* have been seen to vary (especially in South American specimens) to about the same degree. However, the two taxa seem to agree in all other features.

Polystichum rachichlaena Fée, Mém. Fam. Foug. 8: 100. 1857. *P. confluens* Fourn. Mex. Pl. 1: 92. 1872 (syntype from San Rafael, Mexico, *Guillemin s.n.*).

Wet montane forests, not common, 1,600-3,000 m., Baja Verapaz; Sacatepéquez. Mexico (type from Popocatepetl, 3,000 m., *Schaffner 290*).

Plants terrestrial; rhizome stout, erect, amply provided with broad, flaccid, thin brown scales, these concolorous or bicolorous (with a lighter brown margin); leaves to 1 m. long and 0.2 m. broad; petiole to 40 cm. long, stramineous to light brown, scaly (densely so at base), the scales flat and usually flaccid, dark brown, often with a lighter margin, narrowly or broadly lanceolate, these to 2 cm. long and 0.4 cm. broad; lamina bipinnate, chartaceous, narrow-ovate or lanceolate, scarcely reduced at base; rachis lacking a proliferous bud, stramineous or light brown, amply to abundantly scaly, the scales linear or filiform, orange or, rarely, a few with a blackish median stripe, the margins entire or (rarely) minutely setulose; pinnae (22) 24-30 free pairs, 8-12 (16) cm. long, 1.5-2.5 cm. broad, sessile, approximate to subdistant, ascending, basal ones slightly deflexed; pinnules 14-22 free pairs (on the largest pinnae), approximate to crowded or imbricate, subsessile, inequilateral at base, basiscopically cuneate, acroscopically truncate and inconspicuously auriculate (the auricle of basal pinnules often nearly discrete), spinulose at the apex and on the auricle, and often short-spinulose along

the acroscopic margin, the margin subentire to crenulate or serrulate, essentially plane; veins distinct or indistinct, 1- to 3-forked (or pinnately branched in the auricle), often fibrillose-scaly abaxially; sori medial to inframedial, essentially uniseriate, often confluent at maturity; indusia tawny, erose, the margins often involute, persistent, larger ones 1-1.5 mm. broad.

This and some specimens of *P. fournieri* are difficult to separate, and perhaps it might be better to combine the two species. Although the type is supposed to be at the herbarium in Paris, I have been unable to locate it. However, at Paris there is a Schaffner specimen (s.n.) marked simply "Mexico," and determined as *P. rachichlaena* (possibly an isotype). Also at Paris there are two sheets of *Bourgeau 914*, "deserta vieja, vallée de Mexico," determined as *P. rachichlaena* and so cited by Fournier (*loc. cit.*). These specimens rather closely match the type of *P. confluens*, and all of them seem quite distinct from the type of *P. fournieri*, especially in the number of pinnae, spacing and dissection of pinnules, and the length and number of marginal spines. (For further comparison of characters, see discussion of *P. fournieri*.) However, these seem to be differences more of degree than of essence, and some specimens have been seen with characters which tend to be intermediate.

POLYTAENIUM Desvaux

REFERENCES: R. C. Benedict, The genus *Antrophyum*, Bull. Torrey Bot. Club 34: 445-458. 1907; and, The genera of the fern tribe Vittarieae, *op. cit.* 38: 153-190. 1911. R. M. Tryon, Taxonomic Notes IV: Some American vittarioid ferns, Rhodora 66: 110-117. 1964.

Plants small to medium-sized, epiphytic (in ours) or rarely epipetric; rhizome rather thick, short-creeping to ascending, clathrate-scaly, and often clothed with masses of golden-tomentose roots; leaves monomorphic, not articulate, simple and entire, crowded to subfasciculate, rarely more than 50 cm. long and 6 cm. broad, elliptic-lanceolate to oblanceolate or subspatulate; petiole lacking or essentially so; lamina glabrous, fleshy when living, firm-herbaceous to coriaceous when dried, the costa percurrent, prominulous abaxially, flush to immersed and often becoming indistinct to obscure adaxially; venation indistinct to obscure, areolate, the areoles in several series between costa and margin, without free included veinlets; sporangia stalked, slightly to deeply immersed, borne abaxially along the (usually longitudinal) veins, in crooked or forked (rarely reticulate) patterns; indusium and paraphyses lacking; spores trilete, tetrahedral.

Although the species of *Polytaenium* could be included in the genus *Antrophyum* with little or no argument from other pteridologists, I prefer to follow Tryon (1964) in keeping the genera separate. The latter genus has leaves with the costa either lacking or else evident only in the proximal half of the lamina, or if nearly percurrent then

present as a broad band of discolored tissue flush with the leaf surface. The costa in *Polytaenium* is not only percurrent, but is also strongly prominulous along the abaxial side. Paraphyses are abundant along the soral lines in *Antrophyum*, but lacking in *Polytaenium*. Spores in the latter are always trilete and tetrahedral, and although they are similar in the Asian species of *Antrophyum*, they are monolete and bilateral in the American and (most) African species.

As defined above, *Polytaenium* is comprised of about 10 species (some ill defined) and is confined to the neotropics. Three of these occur in Guatemala.

- a. Soral lines deeply immersed in the tissue, in long, straight, mostly continuous lines parallel to the costa; plants of middle elevations, commonly above 1,200 m.
P. lineatum.
- a. Soral lines superficial to shallowly immersed, in long or short, crooked, often interrupted lines subparallel or diagonal to the costa; plants of lowland forests, below 1,000 m.
- b. Laminae oblanceolate to subspatulate, most of them more than 2 cm. broad; longitudinal veins (and thus the areoles) running diagonal to the costa.
P. cajenense.
- b. Laminae elliptic-lanceolate, most of them less than 2 cm. broad; longitudinal veins (and thus the areoles) subparallel to the costa. *P. feei*.

***Polytaenium cajenense* (Desv.) Benedict**, Bull. Torrey Bot. Club 38: 169. 1911. *Hemionitis cajenensis* Desv. Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. 5: 311. 1811. *Antrophyum cajenense* (Desv.) Spreng. Syst. Veg. 4: 67. 1827. *A. discoideum* Kunze, Bot. Zeit. 6: 702. 1848. *P. discoideum* (Kunze) Benedict, Bull. Torrey Bot. Club 38: 169. 1911.

In wet forests or wooded ravines, on tree trunks, 50-900 m.; Alta Verapaz; Izabal. Greater Antilles; southern Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants epiphytic; rhizome short-creeping, densely covered with golden-tomentose roots, and amply provided with light-brown to castaneous, iridescent scales, these linear or linear-lanceolate, 3-7 mm. long; leaves 8-35 cm. long, 1.8-4 cm. broad, sessile or subsessile, crowded to subfasciculate; petiole essentially lacking, the leaf tissue long-decurrent along the costa fully, or nearly, to the base; lamina oblanceolate or subspatulate, reduced abruptly to an acute or acuminate apex, tapering gradually to base, coriaceous to (occasionally) firm-herbaceous, margins plane or, more commonly, somewhat revolute, the costa percurrent, strongly prominulous abaxially, immersed or flush adaxially and usually becoming indistinct toward the apex; veins indistinct or obscure, copiously areolate, the veins diverging at a narrow angle, forming 3-6 series of areoles in a diagonal line between costa and margin; sporangia immersed, borne along the longitudinal, and sometimes the connecting, veins, forming areoles or crooked lines diagonal to the costa.

There has been much confusion between this and *P. brasilianum* (Desv.) Benedict and *P. discoideum* (Kunze) Benedict. See Tryon's discussion of the genus (1964) for a full explanation. Briefly, *P. discoideum* (= true *P. brasilianum*), which is confined to South America, has a very thin lamina with the tissue of the decurrent wings darker than the light-colored costa. *Polytaenium cajenense* (broadly distributed throughout the neotropics and often found in herbaria identified as *P. brasilianum*) has laminae coriaceous (rarely thin), with the wings of tissue concolorous with or lighter in color than the costa. The two species do not differ significantly in any other features and perhaps, more properly, should be considered merely varieties. *Polytaenium guayanense* (Hieron.) Alston (often found in herbaria as *P. cajenense*) is a thin-textured South American species, with narrow, elliptical leaves, tapering subequally to apex and base, easily distinguishable from the spatulate or oblanceolate leaves of the other two species.

Polytaenium feei (Shaffner ex Fée) Maxon, Sci. Surv. Porto Rico and Virgin Is. 6: 405. 1926. *Hemionitis lanceolata* L. Sp. Pl. 1077. 1753. *Antrophyum lanceolatum* (L.) Kaulf. Enum. Fil. 198. 1824. *A. feei* Schaffner ex Fée, Mém. Fam. Foug. 7: 42. 1857. *P. lanceolatum* (L.) Benedict, Bull. Torrey Bot. Club 38: 169. 1911. *nom. illeg.* (not Desv. 1827).

In deep forests or wooded ravines, on tree trunks or large logs, sea level to 500 m., Alta Verapaz; Baja Verapaz; Izabal. West Indies; southern Mexico to Panama; Colombia; the Guianas; Ecuador.

Plants epiphytic; rhizome very short-creeping, densely covered with golden-tomentose roots, and amply provided with castaneous, rather iridescent scales, these linear or linear-lanceolate, 2-5 mm. long; leaves 6-32 cm. long, 0.8-2 cm. broad, erect or pendent, sessile, crowded to subfasciculate; petiole essentially lacking, the leaf tissue long-decurrent along the costa fully to base; lamina elliptic-lanceolate, commonly tapering gradually and subequally to both apex and base, firm-herbaceous to chartaceous, margins plane or scarcely revolute, the costa prominulous and percurrent abaxially, flush to immersed and often indistinct to obscure in the distal portion adaxially; veins indistinct to obscure, copiously areolate, the areoles commonly elongated and essentially oriented parallel to the costa, in 3-5 series; sporangia slightly immersed or nearly superficial, borne mostly along the longitudinal veins, forming rather crooked and broken soral lines subparallel to or slightly diagonal to the costa.

Polytaenium lineatum (Sw.) J. Sm. J. Bot. (London) 4: 68. 1841. *Hemionitis lineata* Sw. Prodr. 129. 1788. *Vittaria lanceolata* Sw. Ges. Naturf. Freunde Berlin Neue Schriften 2: 133. 1799. *Antrophyum lineatum* (Sw.) Kaulf. Enum. Fil. 199. 1824. *Polytaenium lanceo-*

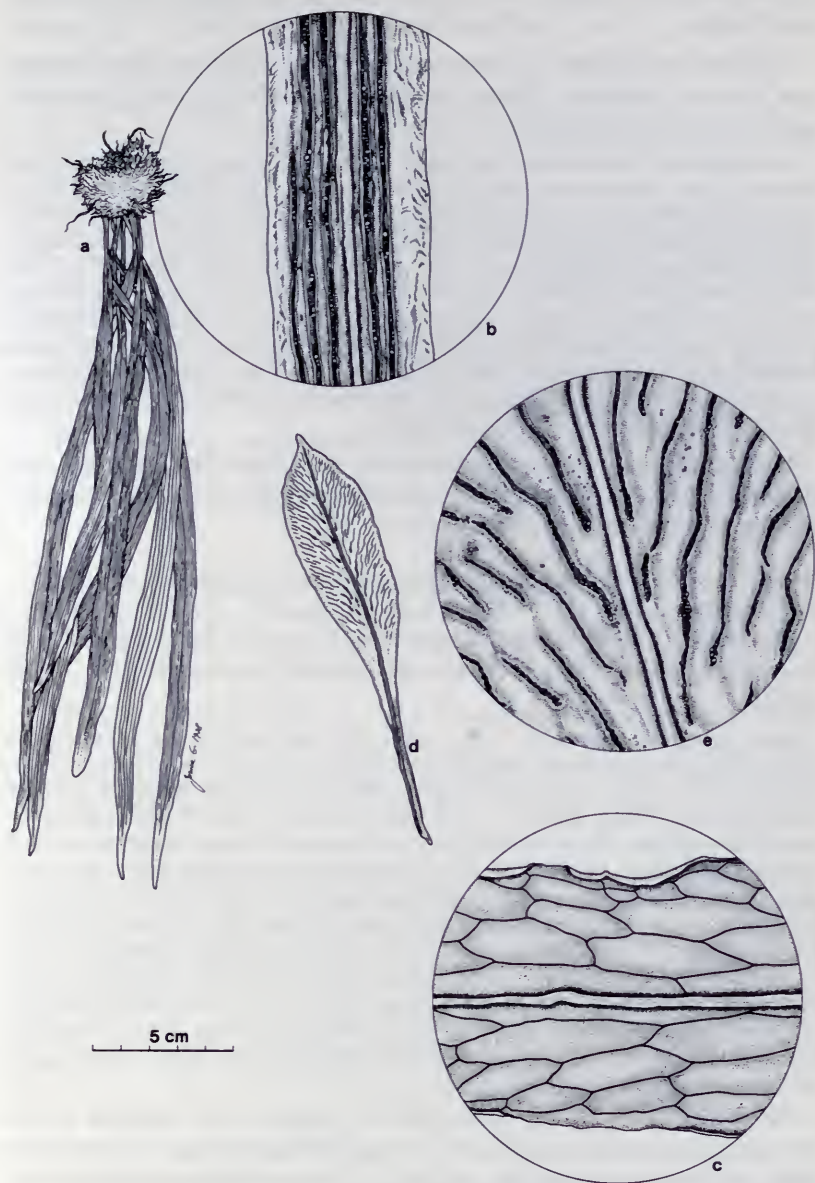


FIG. 68. *Polytaenium*. a-b, *P. lineatum*: a, habit, $\times \frac{1}{2}$; b, portion of lamina, with grooved soral lines; c, *P. feei*, portion of lamina, cleared to show venation; d-e, *P. cajenense*: d, fertile lamina, $\times \frac{1}{2}$; e, portion of fertile lamina, soral lines, $\times 3$.

latum (Sw.) Desv. Mem. Soc. Linn. Paris 6: 218. 1827 (not [L.] Benedict, 1911).

In dense wet forests, on tree trunks, 1,350-1,650 m., Alta Verapaz; San Marcos. Southern Mexico to Panama; Colombia and Venezuela, south to Brazil and Bolivia.

Plants epiphytic; rhizome short, horizontal to ascending, amply provided with brown iridescent, linear to lanceolate scales, these 5-7 mm. long; leaves 10-30 cm. long, 0.5-1.5 cm. broad, sessile, erect or pendent, crowded to subfasciculate; petiole essentially lacking, the leaf tissue long-decurrent along the costa fully to the base; lamina linear to elliptic-lanceolate, tapering gradually and equally to both apex and base (or often broadest just above the middle), subcoriaceous, margins plane to somewhat revolute, the costa prominulous and percurrent abaxially, flush to immersed and often indistinct to obscure in the distal portion adaxially; veins obscure, copiously areolate, the areoles commonly long and narrow and oriented parallel to the costa; sporangia immersed in rather deep continuous grooves along the longitudinal veins, forming 2-4 straight, nearly unbroken soral lines between costa and margin.

The parallel and deeply immersed soral lines make this the most distinctive species in the genus. Fertile specimens should not be confused with those of any other species.

PTERIDIUM Gleditsch ex Scopoli

REFERENCE: R. M. Tryon, Revision of the genus *Pteridium*, Contr. Gray Herb. 134: 1-70. 1941 (reprinted from *Rhodora* 43: 1-31, 37-67. 1941).

Plants terrestrial, commonly 1-3 m. tall; rhizome long-creeping, subterranean, provided with lustrous, brown, pluricellular trichomes, lacking scales; leaves large and coarse, monomorphic, petiolate; petiole not articulate, yellowish to reddish brown, to atropurpureous at base, glabrous or sparsely pubescent, terete to subquadrangular, broadly and shallowly sulcate adaxially; lamina commonly 3- to 4-pinnate, chartaceous to subcoriaceous; pinnae decompound, broad, spreading (often at right angles) to ascending; ultimate segments pubescent or glabrous, numerous, ovate to (more commonly) linear, the margins strongly revolute; veins free; sori marginal, commonly continuous and elongated; sporangia slender-stalked, borne along a marginal commissure which connects the fertile vein tips, between an outer, false, but functional indusium formed by the reflexed, modified segment margin, and an inner (true but nonfunctional) indusium, which may be a continuous or broken membrane, but is more often rudimentary; paraphyses lacking; spores trilete, globose-tetrahedral, finely spinulose, commonly with perine.

Pteridium is a weedy, cosmopolitan genus, with a single species composed of a dozen varieties. It is characterized by the large, coarse, highly divided leaves which are glabrous or variously pubescent, but which lack scales, and by the strongly revolute segments, whose modified margins serve as functional indusia. Three of the varieties occur in Guatemala.

***Pteridium aquilinum* (L.) Kuhn** in v.d. Decken, *Reisen in Ost-Afrika* 3 (3): 11. 1879 (based on *Pteris aquilina* L. Sp. Pl. 1073. 1753).

Characters are those of the genus.

The typical variety is widespread in Europe and Africa, but is not found in the New World. The following key will separate the varieties occurring in Guatemala.

- a. Costae and costules with low, free lobes alternating with many of the ultimate segments; midrib of ultimate segments commonly alate abaxially (the wings membranous, irregular, and often deciduous). *P. aquilinum* var. *arachnoideum*.
- a. Costae and costules lacking free lobes between ultimate segments; midrib of ultimate segments nonalate.
 - b. Ultimate segments sparsely (rarely densely) pubescent abaxially, the trichomes subappressed and rather straight; indusium glabrous (rarely ciliate); midrib of ultimate segments glabrous or abaxially with a few castaneous trichomes. *P. aquilinum* var. *caudatum*.
 - b. Ultimate segments amply to densely villous, the trichomes tortuous and spreading; indusium ciliate and often pubescent; midrib of ultimate segments amply to abundantly provided abaxially with white or castaneous trichomes. *P. aquilinum* var. *feeii*.

***Pteridium aquilinum* var. *arachnoideum* (Kaulf.) Brade**, *Zeitschr. Deutsch. Ver. Wiss. Kunst. S. Paulo* 1: 56. 1920. *Pteris arachnoidea* Kaulf. Enum. Fil. 190. 1824. *Pteridium arachnoideum* (Kaulf.) Maxon, *J. Wash. Acad. Sci.* 14: 89. 1924.

In forests and thickets or, more commonly, on open banks, hillsides, pastures, or forest clearings, 200-2,600 m.; Alta Verapaz; Baja Verapaz; Izabal; Quezaltenango; San Marcos; Zacapa. West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Uruguay and Argentina.

Petiole to 1 m. long, commonly shorter than the lamina; costae and costules commonly bearing free, or nearly free, short and broad lobes between adjacent segments; costules of penultimate segments sparsely to abundantly pubescent abaxially, commonly with dark or bicolorous, septate trichomes, adaxially glabrous or sparsely pubescent with minute, mostly white trichomes; ultimate segments mostly linear, straight or slightly narrowed at base, or decurrent basiscopically, the margins commonly sparsely pubescent, the midrib amply pubescent with dark or bicolorous trichomes and commonly bearing an inconspicuous and irregular (sometimes deciduous) wing on either side abaxially, the tissue between midrib and margin abundantly provided abaxially with fine, whitish, subappressed, arachnoid, trichomes (or very rarely glabrate); indusium ciliate or pubescent, or sometimes glabrate.

This and var. *caudatum* are most closely related, and some intermediates may be found in Guatemala as well as elsewhere throughout the range. Besides the characters used in the key, the two also can often be separated by the degree of pubescence on costules of penulti-

mate segments. In var. *caudatum* the costule is generally glabrous abaxially, or with a few, scattered dark trichomes. In var. *arachnoideum* the costule is sparsely to abundantly pubescent.

***Pteridium aquilinum* var. *caudatum* (L.) Sadeb.** Jahrb. Hamburg. Wiss. Anst. 14 (Beih. 3): 5. 1897 (as to basionym). *Pteris caudata* L. Sp. Pl. 1075. 1753. *Pteridium caudatum* (L.) Maxon, Proc. U.S. Natl. Mus. 23: 631. 1901.

In woods and thickets, or in clearings or on open slopes, sea level to 2,800 m.; Baja Verapaz; Izabal; Jalapa; Petén; Sacatepéquez; Sololá; Zacapa (probably to be expected in many other departamentos in Guatemala). West Indies; Florida; Mexico to Panama; Colombia; Venezuela.

Petiole to 1.5 m. long, about as long as the lamina; costae and costules without free lobes between segments; costules of penultimate segments glabrous to sparsely pubescent abaxially, with white, castaneous, or bicolorous trichomes, adaxially glabrous or with a few, short, dark trichomes; ultimate segments mostly linear, straight or slightly narrowed at base, or decurrent basiscopically, the margins glabrous or sparsely pubescent, the midrib nonalate, glabrous or sparsely provided with castaneous or bicolorous, septate trichomes, the tissue between margin and midrib glabrous to abundantly pubescent abaxially with subappressed, often arachnoid trichomes; indusium glabrous or (very rarely) sparsely ciliate.

***Pteridium aquilinum* var. *feeii* (Schaffn. ex Fée) Maxon ex Yuncker,** Field Mus. Nat. Hist. Bot. Ser. 17 (4): 308. 1938. *Pteris aquilina* L. var. *pubescens* Kunze, Linnaea 13: 142. 1839 (as to plant, not basionym: *P. lanuginosa* Spreng.) *Pteris aquilina* L. var. *pubescens* Spreng. ex Liebm. Kongel. Danske. Vidensk. Selsk. Skr., Naturv. Afd. V, 1: 226 (seors. 74) 1849. *Pteris feeii* Schaffn. ex Fée, Mém. Fam. Foug. 8: 73. 1857. *Pteridium feeii* (Schaffn. ex Fée) Faull, Contr. Arnold Arbor. 11: 87. 1938.

In woods and thickets, and in clearings, pastures, and open slopes, 1,700-3,800 m.; Baja Verapaz; Chimaltenango; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; Sololá; Totonicapán. Mexico; Honduras; El Salvador.

Petiole to 1 m. long, commonly shorter than the lamina; costae and costules without free lobes between the segments; costules of penultimate segments amply to abundantly pubescent abaxially, with white or castaneous, septate trichomes, adaxially sparsely to amply provided with shorter, white or orange trichomes; ultimate segments mostly elongate-deltoid, straight or subequally dilated on both sides at base, the margins commonly pubescent, the midrib nonalate, amply to abundantly provided with white or castaneous, septate trichomes, the tissue between margin and midrib amply to densely villous; indusium ciliate and commonly pubescent.

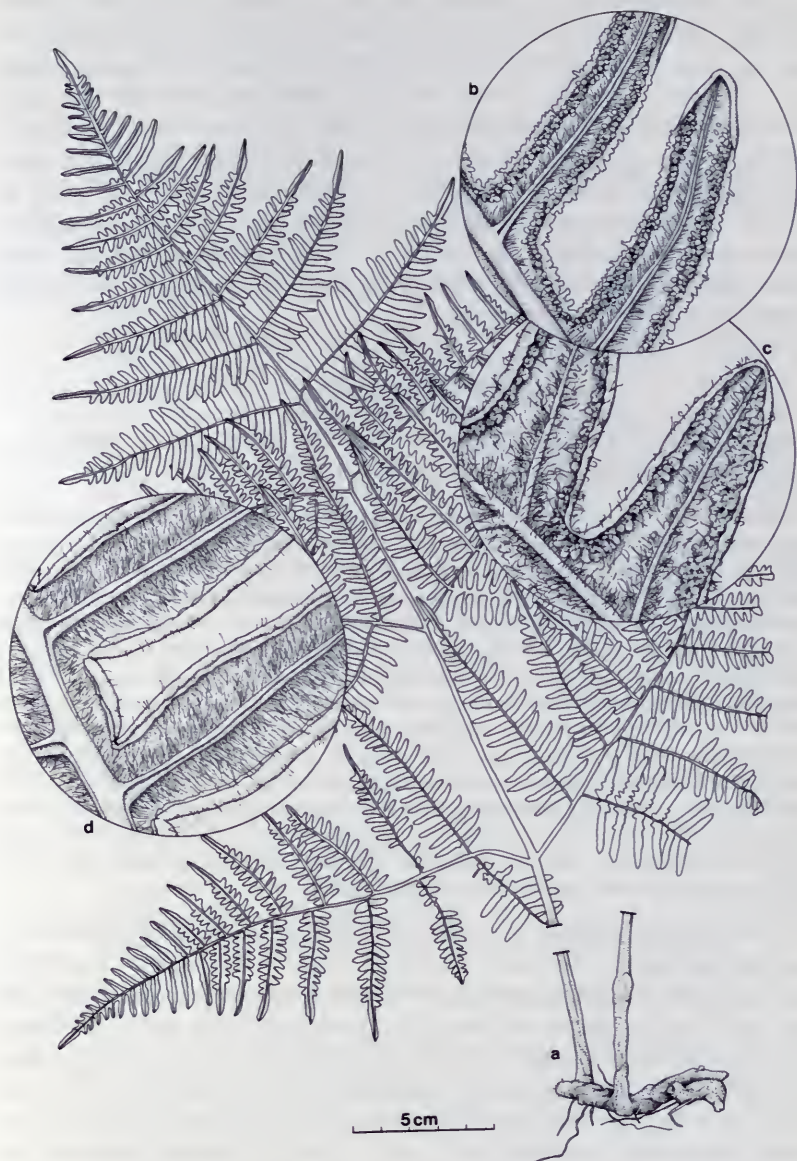


FIG. 69. *Pteridium aquilinum*. a-b. *var. caudatum*: a, habit, $\times \frac{1}{2}$; b, ultimate segments, $\times 6\frac{1}{2}$; c, *var. feei*, ultimate segments, $\times 6\frac{1}{2}$; d, *var. arachnoideum*, ultimate segments, $\times 6\frac{1}{2}$.

This variety is readily distinguished from the others in Guatemala by the pubescence on the abaxial surface of ultimate segments. In var. *feeii* the trichomes are long, tortuous, and spreading, and usually copious. In vars. *arachnoideum* and *caudatum* the amount of pubescence may vary on the abaxial surface, but the individual trichomes are finer, straighter, and subappressed. Also, var. *feeii* can often be distinguished by its typically broader and shorter ultimate segments, most of these being elongate-triangular (two to three times as long as broad), spreading rather equally to a broad base. Many segments of vars. *arachnoideum* and *caudatum* are linear, or linear-oblong (many times longer than broad), and often inequilateral at base—much longer-decurrent basiscopically.

PTERIS Linnaeus

REFERENCE: R. M. Tryon, *Pteris*, in: The ferns of Peru—Polypodiaceae, Contr. Gray Herb. 194: 188-210. 1964.

Plants terrestrial; rhizome commonly stout, scaly, long-creeping to ascending, or erect; leaves usually very large, essentially monomorphic, petiolate, pubescent to glabrous, but at least sparsely scaly; petiole not articulate, scaly at least at base, terete to subquadrangular, variously sulcate adaxially, at least distally; lamina 1- to 4-pinnate, firm-herbaceous to subcoriaceous, often subternate, with each of the basal pinnae nearly as large as the rest of the lamina; pinnae spreading at a broad (often 90°) angle, or ascending, the basal pair in many species forking near the base; costae of penultimate segments deeply sulcate adaxially, the parallel ridges frequently bearing spinelike awns, one each at the base of ultimate segments; veins free or sparsely to copiously anastomosing, the areoles lacking free, included veinlets; sori marginal, short to (more commonly) greatly elongated, in a few species extending from segment tip to and around the sinus between adjacent segments; indusium continuous along the sorus, formed by the reflexed, modified (often scarious) segment margin; sporangia stalked, borne on a marginal commissure which connects the fertile vein tips; paraphyses usually numerous; spores commonly trilete and tetrahedral, with perine.

Pteris is a pantropical (to subtropical) genus of about 250 species. It is characterized by the usually large and coarse leaves with basal pinnae (at least in decompose species) very strongly produced and each one nearly as large as the rest of the lamina. This gives a ternate appearance to the leaves (or even subpalmate, in a few species where the pinnae are again strongly produced on the basiscopical side). The genus may be even more readily recognized by the continuous, usually greatly elongated, marginal sori, which typically extend from near the segment tip almost or quite to the sinus between adjacent segments.

Some species of *Pteris* might be mistaken for *Lonchitis*, under which see further discussion.

- a. Pinnae simple and undivided or (in *P. cretica*) a few of them forking once (rarely twice) near the base.
- b. Veins (many of them) anastomosing toward the pinna margin; sterile margins entire throughout; larger pinnae 2-4 cm. broad. *P. grandifolia*.
- b. Veins free; sterile margins serrulate or serrate, at least toward the pinna apex; pinnae 0.3-1.8 (2) cm. broad.
- c. Pinnae not articulate, 1-5 pairs, the basal ones (and often others) forked, with the ultimate segments subequal. *P. cretica*.
- c. Pinnae articulate to the rachis, numerous, all of them simple, unbranched. *P. longifolia*.
- a. Pinnae regularly pinnatifid, pinnate, or more highly divided.
- d. Venation essentially free.
- e. Basal pinnae pinnately arranged, the numerous pinnules deeply pinnatisect to 2- to 3-pinnate.
- f. Apices of ultimate segments blunt and crenate; costae of penultimate segments adaxially provided with long, subulate awns; rachis smooth, minutely and sparsely pubescent, to glabrate. *P. muricella*.
- f. Apices of ultimate segments acute, cuspidate, and (usually) serrate; costae of penultimate segments adaxially provided with short, blunt to subacute awns; rachis commonly muricate or spinulose, sparsely to amply scaly and/or pubescent. *P. muricata*.
- e. Basal pinnae 1-forked, each branch pinnatisect.
- g. Pinnae (excluding the basal pair) strongly and gradually reduced at base, the basal segments often merely auricles adnate or decurrent at base of costa; veins (1 or 2 basiscopic ones) arising from the costa between adjacent ultimate segments. *P. pungens*.
- g. Pinnae (excluding the basal pair) slightly or not at all reduced at base, the basal segments at least $\frac{1}{2}$ as long as the longest central ones; veins all arising from the segment midrib (or occasionally the basal basiscopic one borne on the costa near its junction with the midrib).
- h. Ultimate segments linear or narrow-oblong, spreading at a broad (often 90°) angle from the costa, subequilateral at base; rhizome scales bicolorous, with erose or ciliolate margins; awns along costa (adaxially) long and conspicuous. *P. quadriaurita*.
- h. Ultimate segments commonly elongate-triangular, obliquely spreading, inequilateral at base (acroscopically straight or rounded toward the midrib, basiscopically more strongly produced and curving away from the midrib); rhizome scales concolorous, entire; awns inconspicuous or lacking. *P. paucinervata*.
- d. Venation fully or partially areolate (at least a single row of areoles along the costae of penultimate segments).
- i. Lamina 2-pinnate (or 3-pinnate as to the basal pinnae), the ultimate segments free, often stalked; axes lacking awns. *P. mexicana*.
- i. Lamina 2-pinnate-pinnatifid or 3-pinnate-pinnatifid, the ultimate segments (or lobes) joined; axes of penultimate segments adaxially awned at the bases of ultimate segments.
- j. Veins free except for a single row of areoles along the costa of penultimate segments; basal pinnae 1-forked, each branch pinnatisect. *P. biaurita*.
- j. Veins predominantly areolate; basal pinnae pinnately arranged, the numerous pinnules pinnatisect to 2-pinnate-pinnatisect.

- k. Axis of penultimate segments with 2 or more costular areoles between midribs of adjacent ultimate segments; lamina essentially glabrous. *P. altissima*.
- k. Axis of penultimate segments with a single costular areole between midribs of adjacent ultimate segments; lamina sparsely to amply provided with minute, castaneous, septate trichomes, at least abaxially.
 - l. Penultimate segments truncate or broadly cuneate at base, most of them oblong-lanceolate, with margins essentially parallel and then abruptly narrowing at the apex; tips of most ultimate segments pointed strongly toward apex of pinna (or penultimate segment). *P. podophylla*.
 - l. Penultimate segments commonly sharply decurrent along the costa at base, lanceolate or narrow-ovate, broadest at or near the base and tapering gradually to apex; tips of most ultimate segments straight, or only slightly curved. *P. polita*.

Pteris altissima Poir. in Lam. Encycl. Méth. Bot. 5: 722. 1804. *P. kunzeana* Ag. Recens. Sp. Gen. Pteridis 62. 1839. *Litobrochia altissima* (Poir.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 135. 1850-1852.

In forests, thickets, and wooded ravines, often in rocky soil, and along streams and rivers, 100-1,100 m.; Alta Verapaz; Chimaltenango; Escuintla; Izabal; Petén; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa. West Indies; Mexico to Panama; Colombia to the Guianas, south to Brazil and Bolivia.

Plants terrestrial; rhizome stout, creeping to ascending or erect, provided with ovate to lanceolate scales, these 1-3 mm. long, bicolorous, lustrous, castaneous to blackish, with broad, dull, light-brown, erose to ciliolate margins; leaves crowded to caespitose, mature ones 0.8-2 m. long, petiolate; petiole 40-90 cm. long, about as long as the lamina, stout (often 1 cm. thick), terete to quadrangular, sulcate adaxially, stramineous to yellow- or gray-brown, essentially glabrous, but with a few bicolorous scales at base; lamina firm-herbaceous to chartaceous, glabrous, essentially pinnate-pinnatifid, but 2-pinnate-pinnatifid as to basal (and often a few more) pinnae, deltoid, terminating in a broad-based, pinnatifid, apical segment; rachis stramineous, glabrous, sulcate adaxially; pinnae stalked (or some distal ones sessile), the basal (and 1 or 2 other) pairs deltoid, pinnate-pinnatifid, the rest deltoid or ovate, broadest (or nearly so) at base, tapering to a caudate or subcaudate apex; costae of penultimate segments provided adaxially with small, acute awns, one each at the base of an ultimate segment; ultimate segments elongate-deltoid, acute to acuminate, joined by a usually broadly rounded sinus, margins mostly subentire, but sharply serrate toward the segment apex; venation copiously areolate, most of the areoles rather broad, pentagonal or hexagonal, a line of 2-6 of them borne along the costa between midribs of adjacent ultimate segments; sori elongated, commonly extending completely around the sinus between segments, but terminating short of the serrate tips; indusium whitish, yellowish, or pale brown, entire.

Pteris biaurita L. Sp. Pl. 1076. 1753.

In forests, thickets, and wooded ravines, or sometimes on open banks or cliffs, 220-750 m.; Escuintla; Petén; Quezaltenango; San Marcos; Santa Rosa; Suchitepéquez. West Indies; southern Mexico; British



FIG. 70. *Pteris*. a-b, *P. biaurita*: a, habit, $\times \frac{1}{2}$; b, portion of pinna, showing sori and venation, $\times 6\frac{1}{2}$; c, *P. altissima*, portion of pinna (adaxial side) showing venation and configuration of costa; d, *P. grandifolia*, fertile subapical pinna, $\times \frac{1}{2}$; e, *P. polita*, fertile subapical pinna, $\times \frac{1}{2}$; f, *P. podophylla*, sterile subapical pinna, $\times \frac{1}{2}$.

Honduras; El Salvador; Nicaragua to Colombia and the Guianas, south to Brazil and Peru; Old World tropics.

Plants terrestrial; rhizome stout, erect to ascending, provided with ovate to lanceolate scales, these 1-3 mm. long, bicolorous, lustrous-castaneous to blackish, with broad, dull, light-brown, erose to ciliolate margins; leaves crowded to subcaespitose, 0.6-1.3 m. long, long-petiolate; petiole 40-70 cm. long, equaling or somewhat longer than the lamina, stout, terete to subquadrangular, sulcate adaxially, stramineous to light brown, essentially glabrous, but with a few bicolorous scales toward the base; lamina firm-herbaceous, glabrous, essentially pinnate-pinnatisect, but the basal pair of pinnae 1-forked; rachis stramineous, glabrous, sulcate adaxially; pinnae 5-13 pairs, sessile or subsessile, the basal pair forked, the branches unequal or subequal, each of them pinnatisect, the other pinnae simple, pinnatisect, gradually tapering to a caudate apex, scarcely or not at all reduced at base; costae provided adaxially with minute, acute awns (these often broken off in dried specimens), one each at the base of an ultimate segment; ultimate segments narrow-oblong, falcate or subfalcate, obtuse, the margins and apex subentire; veins free, except for a single row of areoles along the costa of penultimate segments (or very rarely a few veins anastomosing along the costal areole), commonly 1-forked; sori elongated, often extending the length of the segment from sinus to tip; indusium scarious to pale yellow, entire.

***Pteris cretica* L. Mantissa Pl. 130. 1767.**

In forests, thickets, and wooded ravines, often on shaded slopes and river banks, 1,400-3,000 m.; Alta Verapaz; Chimaltenango; Guatemala; Huehuetenango; El Progreso; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Sololá; Zacapa. Florida; Jamaica; Mexico; El Salvador; Costa Rica; Brazil; Peru; Argentina; temperate and tropical regions of the Old World.

Plants terrestrial; rhizome short-creeping, provided with linear, castaneous scales 1-2 mm. long; leaves densely crowded, 40-100 cm. long, 15-30 cm. broad, long-petiolate; petiole 20-70 cm. long, commonly longer than the lamina, wiry, stramineous and subquadrangular, or light brown and terete toward the base, sulcate adaxially, glabrous; lamina 1-pinnate, with 1-5 pairs of simple or 1- (2-) forked pinnae and a conform apical segment, the tissue firm-herbaceous to chartaceous and essentially glabrous; rachis stramineous, glabrous, but occasionally with a few, minute, castaneous, filiform scales scattered abaxially; pinnae sessile or short-stalked, simple, or often 1-3 pairs forked once (very rarely twice) near the base, larger ones 10-22 cm. long and 0.8-1.8 (2) cm. broad, lanceolate or linear-lanceolate, narrowly acute to attenuate, cuneate or adnate at base, the sterile margins serrulate or serrate (at least toward pinna apex); veins free, simple or 1-forked; sori long, continuous, borne on both margins nearly from apex to base; indusium commonly pale, entire.

This is a rather common fern in Mexico and Guatemala, but is sparsely scattered throughout the rest of Central America and South America, where it probably has escaped from cultivation. It is also common in temperate and tropical areas of the Old World, occurring in parts of Europe, as well as in Asia and Africa. *Pteris cretica*, including

some strikingly colored varieties, has been a rather popular house and garden plant around the world.

Pteris grandifolia L. Sp. Pl. 1073. 1753. *Litobrochia grandifolia* (L.) J. Sm. J. Bot. (London) 4: 163. 1841.

In thickets and forests, commonly on hillsides and embankments, sea level to 1,350 m.; Alta Verapaz; Baja Verapaz; Izabal; Petén; Santa Rosa. West Indies; Colombia; Venezuela; Brazil; Ecuador; Peru.

Plants terrestrial; rhizome stout, woody, creeping, provided with linear, attenuate, orange to light-brown scales, these 1-3 mm. long; leaves approximate to well-spaced, commonly 2-4 m. long, 0.3-0.5 m. broad, long-petiolate; petiole 0.3-1.2 m. long, stout, terete, stramineous, glabrous, but with some linear scales near the base; lamina 1-pinnate, with 10-20 pairs of entire pinnae (on mature laminae) and a conform apical segment, firm-herbaceous to chartaceous, essentially glabrous; rachis stramineous, glabrous, or with a few, scattered, pale, hairlike scales near the pinna axils abaxially; pinnae subsessile or short-stalked, larger ones 16-35 cm. long and 2-4 cm. broad, lanceolate or linear-lanceolate, narrowly acute to acuminate, broadly cuneate or rounded at base, the margins entire throughout; veins simple or 1-forked, approximate and parallel for most of their length, many of them anastomosing near the margin (but merging much less frequently on narrower, fertile pinnae); sori long, continuous, borne on both margins nearly from apex to base; indusium pale, subentire.

See discussion of *P. mexicana* for comparison of characteristics.

Pteris longifolia L. Sp. Pl. 1074. 1753. *P. longifolia* var. *angusta* Christ, in Krug in Urban, Bot. Jahrb. Syst. 24: 98. 1897 (type from Cuba, *Eggers 5170b*). *P. longifolia* var. *angusta* Christ ex Donn.-Sm. Bot. Gaz. 37: 423. 1904 ("type" from Cubilguitz, Alta Verapaz, *Tuerckheim* [ed. Donn.-Sm. No. 8344b]; not a valid type, see discussion below).

In forests or thickets, commonly on rocky cliffs or slopes, sea level to 2,800 m.; Alta Verapaz; Chiquimula; Huehuetenango; Izabal; Petén; Sololá. West Indies; Mexico; British Honduras; Honduras; Venezuela. A nearly glabrous variant occurs in Florida and the Bahamas.

Plants terrestrial; rhizome short-creeping to ascending, densely covered with linear, orange to pale-brown scales 2-3 mm. long; leaves densely crowded to subfasciculate, 40-120 cm. long, 9-28 cm. broad, petiolate; petiole 6-50 cm. long, commonly much shorter than the lamina, wiry or stout, stramineous to gray-brown, terete, densely provided (in ours) with linear, light-brown, attenuate scales, these tortuous, spreading, 2-4 mm. long; lamina 1-pinnate, elliptic to lanceolate, tapering to apex and base, with numerous, simple pinnae and a conform apical segment, the tissue chartaceous to subcoriaceous and essentially glabrous, but (in ours) commonly pubescent-scaly on the axes abaxially; rachis stramineous to yellow-brown, abundantly provided (in ours) with pale-orange or light-brown scales, as on the petiole; pinnae 4-16 cm. long, 0.3-0.9 cm. broad, spreading from the rachis at a broad (often 90°) angle, linear, truncate or cordate at base, acute to attenuate at apex, with margins serrulate to serrate, articulate to the rachis, the point of

articulation often nodose and discolored; veins free, simple or 1-forked; sori long, continuous, commonly running along each margin from apex to base; indusium scarious, undulate, and conspicuously erose.

There have been several varieties of this species described, of which ours is the typical. Representing the species in Florida and the Bahamas is var. *bahamensis* Hieron., which is glabrous, or nearly so, on costae and rachis. Christ proposed his var. *angusta* on the basis of its supposedly narrower pinnae and more scaly axes—both characters merely quantitative, and appearing to me to be neither significant nor consistent. Tuerckheim's collection (ed. Donn.-Sm. 8344b) from Alta Verapaz is not a valid type. Donnell-Smith described this variety in 1904, apparently unaware that Krug had published a Christ description 7 years before, citing Eggers 5170b, from Cuba, as type of the variety. The earlier description was valid, thus the Eggers collection is the valid type.

A species with which *P. longifolia* often has been confused, in both the New and Old World, is *P. vittata* L. Both species have laminae tapering strongly to apex and base, with numerous, linear pinnae. However, *P. longifolia* is confined to the New World and may be easily distinguished by its pinnae being articulate to the rachis. Furthermore, the rachis is densely scaly, and the indusia are conspicuously erose. *Pteris vittata* is essentially an Old World species, but it escapes from cultivation and becomes naturalized in scattered areas of the neotropics. In this species pinnae are not articulate, indusia are subentire, and axes commonly are only sparsely scaly.

Pteris mexicana (Fée) Fourn. Mex. Pl. 117. 1872. *Litobrochia mexicana* Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 136. 1850-1852. *P. pulchra* Schlecht. and Cham. Linnaea 5: 614. 1830 (not Vell. 1827) *nom. illeg.*

In thickets and forests, 50-1,350 m.; Alta Verapaz; Chimaltenango; Escuintla; Huehuetenango. Mexico; El Salvador.

Plants terrestrial; rhizome erect or ascending, provided with lanceolate to ovate, bicolorous scales, these about 2 mm. long, castaneous to blackish, with broad, light-brown, ciliate or erose margins; leaves crowded, 1-2 m. long, petiolate; petiole to 75 cm. long, nearly equaling the lamina, stout, terete, sulcate adaxially, stramineous or yellow-brown, glabrous, but with a few bicolorous scales at base; lamina 2-pinnate (or 3-pinnate as to basal pinnae), becoming pinnate distally and terminating in a pinna-like apical segment, firm-herbaceous, essentially glabrous, but often very minutely septate-pubescent along the axes abaxially; rachis stramineous to yellow-brown; pinnae short-stalked, most of them again pinnate (or basal ones 2-pinnate at their bases), the costae sulcate adaxially, but without awns; ultimate segments well-spaced, lanceolate, narrowly acute to acuminate, subfalcate, sessile or subsessile, ascending, inequilateral at base, cuneate acroscopically, more strongly produced and short-decurrent basiscopi-

cally; the sterile margins broadly serrate; veins freely anastomosing, the areoles short and broad along the costule, becoming longer and narrower toward the margin; sori long, continuous, borne on both margins from the segment base, but terminating somewhat short of its apex; indusium yellowish or pale green.

This is a species with very large leaves, and on many herbarium sheets only parts of the lamina are represented. Where only the simply pinnate distal portion of the leaf is available, this could be confused with *P. grandifolia*, which is simply pinnate throughout. However, veins in *P. mexicana* are much more abundantly areolate, the areoles about as broad as long at the midrib, and become longer and narrower toward the margin. In pinnae of *P. grandifolia* none of the veins merge near the midrib, but only begin to merge toward the margin. The two species also differ markedly in their rhizome scales, those of *P. grandifolia* being concolorous and subentire, while scales of *P. mexicana* are bicolorous, with broad, lighter colored, erose or ciliolate margins.

Pteris mexicana is most closely related to (and may be conspecific with) *P. haenkeana* Presl of South America. Leaves of the latter, in the few collections I have examined, are coarser in texture, and the veins thicker and more prominulous, but beyond this there is little to distinguish the two. Significantly, *P. haenkeana* also has the same, rather distinctive, rhizome scales as *P. mexicana*.

***Pteris muricata* Hook. Sp. Fil. 2: 193. 1858.**

In forests, commonly on slopes or ravine banks, 1,800-2,600 m.; Alta Verapaz; Quezaltenango; San Marcos; Zacapa. Southern Mexico; Nicaragua; Costa Rica; Panama; Colombia; Ecuador; Peru; Bolivia.

Plants terrestrial; rhizome creeping to ascending, provided with ovate or lanceolate scales, these 2-4 mm. long, bicolorous, lustrous-castaneous, with broad, lighter brown, erose margins; leaves approximate, to 2 m. long, long-petiolate; petiole to ca. 1 m. long, equaling or longer than the lamina, stout, terete, sulcate adaxially, stramineous to yellow or gray-brown, or darker at very base, sparsely and minutely spinulose or muricate and sparsely and deciduously pubescent-scaly; lamina chartaceous to subcoriaceous, sparsely to abundantly filiform-scaly and/or pubescent along the axes abaxially, essentially pinnate-pinnatisect, but 3- to 4-pinnate as to the greatly enlarged basal (and rarely also the next) pair of pinnae; rachis stramineous to light brown, sulcate adaxially, commonly sparsely to densely muricate or spinulose, and sparsely to amply provided with castaneous, filiform scales and/or simple, septate, castaneous trichomes (but these often deciduous on mature plants); pinnae short-stalked, those above the enlarged basal pair deeply pinnatisect, linear or linear-lanceolate, acuminate or attenuate; costae (of penultimate segments) provided adaxially with short, subacute to blunt awns, 1 each at the base of an ultimate segment, abaxially with castaneous scales or simple trichomes as on the rachis; ultimate segments subfalcate, acute, the apex serrate, commonly cuspidate; veins free, 1-forked, the basal basiscopical one typically arising from the costa (not from the segment midrib); sori elongated, often extending along both margins nearly from base to tip; indusium very pale green to whitish, entire.

With this should perhaps be included *P. deflexa* Link of South America. The two supposedly differ only in texture and amount of pubescence, and in smooth *vs.* muricate axes, but these characters seem rather inconstant. Equally similar are *P. coriacea* Desv. and *P. inermis* (Rosenst.) de la Sota, also of South America. A taxonomic revision of the entire complex is needed, to determine whether any or all of the taxa are truly distinct.

In Guatemala, *P. muricata* might be confused with *P. muricella*, which it resembles superficially. See discussion of the latter for further comparison.

***Pteris muricella* Fée, Mém. Fam. Foug. 8: 73. 1857.**

In wet forests, commonly on slopes or ridges, 900-2,000 m.; Guatemala; San Marcos. Southern Mexico; El Salvador; Nicaragua; Costa Rica; Panama.

Plants terrestrial; rhizome ascending to erect, provided with ovate or lanceolate scales, these 3-6 mm. long, concolorous, orange to dark brown, the margins entire; leaves subfasciculate, to 1.3 m. long, long-petiolate; petiole to ca. 75 cm. long, equaling or longer than the lamina, yellowish to dark brown, terete or subquadrangular, sulcate adaxially, glabrous, or provided with a few, scattered, minute trichomes; lamina firm-herbaceous, tissue glabrous, but with a few, scattered, yellowish or light-brown, septate trichomes along the axes abaxially, essentially pinnate-pinnatisect, but 3- (4-) pinnate as to the greatly enlarged basal pair of pinnae; rachis stramineous to dark brown, sulcate adaxially, smooth, sparsely and minutely pubescent or glabrate abaxially; pinnae sessile to subsessile, or the basal pair short-stalked, those above the enlarged basal pair deeply pinnatisect, lanceolate or elliptic-lanceolate, short-acuminate; costae (of penultimate segments) adaxially provided with long, subulate awns, one each at the base of ultimate segments, abaxially glabrous or sparsely and minutely pubescent; ultimate segments essentially straight, obtuse, the apex broadly crenate; veins free, 1-forked, the basal basicopic one arising from the segment midrib or at its juncture with the costa; sori short to somewhat elongated, usually not reaching too near the base or tip of the segment; indusium tawny to dark brown, the margins entire.

In general aspect and leaf architecture, this may be compared with *P. muricata*, but there the resemblance ends. Besides the features used in the key, the two species differ in other important respects. Rhizome scales in *P. muricata* are distinctly bicolorous and strongly erose, and most ultimate segments have their basal basicopic veinlets arising not from the segment midrib, but from the costa on which the segment is borne. In *P. muricella* the rhizome scales are concolorous and entire, and the basal basicopic veinlet is borne near or at the base of the segment midrib. Leaf texture differs as well, with the lamina in *P. muricata* generally chartaceous to subcoriaceous, whereas in *P. muricella* it is never more than firm-herbaceous.

***Pteris paucinervata* Fée, Mém. Fam. Foug. 8: 73. 1857.**

In forests, on slopes, and in wooded ravines, 1,200-2,800 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; El Progreso; Quezaltenango; San Marcos; Sololá. Mexico; El Salvador; Nicaragua; Costa Rica.

Plants terrestrial; rhizome erect or ascending, provided with lanceolate or linear-lanceolate, attenuate, amber scales, these (4) 5-10 mm. long, concolorous, with entire margins; leaves subcaespitose, 0.5-1.2 m. long, petiolate; petiole to 70 cm. long, about as long as the lamina, wiry or stout, terete abaxially, flattened to broadly sulcate adaxially, yellow to (more commonly) deep reddish brown, glabrous; lamina thin-herbaceous to chartaceous, glabrous or very minutely and sparsely pubescent, with 3-6 (7) pairs of pinnae and a subconform apical segment, essentially pinnate-pinnatisect to nearly 2-pinnate, but the basal (rarely the next) pair of pinnae 1-forked; rachis stramineous to reddish brown, sulcate adaxially, glabrous, smooth; pinnae sessile or subsessile, the basal pair forking, the branches unequal or subequal, each of them very deeply pinnatisect, the other pinnae simple, deeply pinnatisect (or, in larger pinnae, a few proximal segments cut fully to the costa), tapered gradually to a caudate or subcaudate apex, scarcely or not at all reduced to base (if somewhat reduced then the basal segments commonly at least $\frac{1}{2}$ the length of the largest segments); awns along the adaxial side of the costa very short and inconspicuous, or (more commonly) lacking; ultimate segments obliquely spreading from the costa, most of them elongate-triangular, straight to falcate, obtuse to acute, subentire to crenate, inequilateral at base, acroscopically straight, or rounded toward the midrib, basiscopically more strongly produced and curving away from the midrib (and on the few free segments often decurrent along the costa); veins free, mostly 2-4 mm. apart, simple to 1-forked, all arising from the midrib (or the basal basiscopic one occasionally borne on the costa near its juncture with the midrib); sori short to elongated, often extending the length of the segment from sinus nearly to tip; indusium pale yellow or whitish, subentire.

***Pteris podophylla* Sw. J. Bot. (Schrader) 1800 (2): 67. 1801.**

In forests, commonly in ravines, on slopes, or river banks, 1,300-1,700 m.; Alta Verapaz; Huehuetenango; Quezaltenango. Greater Antilles; southern Mexico; Nicaragua; Costa Rica; Panama; Colombia; Venezuela.

Plants terrestrial; rhizome not seen (reportedly stout and creeping); leaves (mature ones) 1.5-4 m. long, petiolate; petiole to 2 m. long, about as long as the lamina, stout, often over 1 cm. thick, terete to subquadrangular, flattened or sulcate adaxially, yellowish to dark reddish brown, sparsely to amply appressed pubescent, or glabrate, but with a few, scattered scales at base, these 2-5 mm. long, rigid, castaneous to blackish, with a broad, light-brown, often deciduous margin; lamina firm-herbaceous to subcoriaceous, sparsely to amply pubescent, at least on the abaxial surface, subternately decompound, the basal pinnae about as large as the rest of the lamina, these pinnate-pinnatifid to 2-pinnate-pinnatifid (and often 2-partite near the base, thus the lamina often appearing subpalmately divided); rachis stramineous to dark yellowish brown, provided (at least in the adaxial grooves) with appressed, septate, castaneous trichomes; pinnae numerous, the basal pair stalked and decompound, the rest pinnatifid; penultimate segments truncate to broadly cuneate at base, oblong, the sides parallel for most of their

length and then narrowing rather suddenly to the acuminate apex, the costae adaxially provided with septate, castaneous trichomes (at least toward the base) and with small, acute awns, one each at the base of an ultimate segment; ultimate segments broad, joined by an acute sinus, 1-2 (3) times as long as broad, the tips of most of them curving sharply and pointing toward the apex of the pinna (or penultimate segment), sterile margins strongly apiculate-serrate; venation copiously areolate, and with a single long areole along the costa between midribs of adjacent ultimate segments; sori short to somewhat elongated, extending from the sinus $\frac{1}{4}$ - $\frac{3}{4}$ of the distance to the tip, not truly continuous around the sinus (but often appearing so); indusium whitish to gray, or yellowish in age, subentire.

This is easily confused with *P. polita*, under which see further comparison.

Pteris polita Link. Hort. Reg. Bot. Berol. 2: 30. 1833. *Pteris propinqua* Ag. Recens. Sp. Gen. Pteridis 65. 1839. *P. apicalis* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 230 (seors. 78). 1849 (type from Mirador, Mexico, *Liebmann 2597*).

In forests, thickets, and wooded ravines, commonly on slopes, often along shores of lakes or ponds, 100-2,800 m.; Baja Verapaz; Chimaltenango; Chiquimula; Izabal; Jutiapa; El Progreso; Quezaltenango; El Quiché; San Marcos; Santa Rosa; Suchitepéquez; Zacapa. Jamaica; Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants terrestrial; rhizome stout, decumbent or erect, provided with bicolorous scales, these 2-4 mm. long, castaneous to lustrous black, with light-brown or grayish, erose margins; leaves 0.5-2 m. long, petiolate; petiole 30-90 cm. long, about as long as the lamina, wiry to stout, stramineous to gray-brown, or darker at the base, terete to subquadrangular, flattened or sulcate adaxially, minutely and sparsely pubescent or (most often) glabrate, but with a few, scattered scales at base; lamina firm-herbaceous to subcoriaceous, minutely pubescent abaxially, subternately decompose, the basal pinnae about as large as the rest of the lamina, these pinnate-pinnatifid to 2-pinnate-pinnatifid (and often 2-partite near the base, thus the lamina often appearing subpalmately divided); rachis stramineous to dark yellowish brown, sparsely provided with castaneous, septate trichomes; pinnae numerous, the basal pair stalked and decompose, the rest pinnatifid; penultimate segments (most of them) narrowly decurrent along the costa at base (and sometimes even onto the next axis below), lanceolate or narrow-ovate, broadest at base or in the lower portion and tapering gradually to a narrowly acute or acuminate apex, the costae adaxially glabrous, but provided with small, acute awns, one each at the base of an ultimate segment, abaxially glabrate or sparsely and minutely pubescent; ultimate segments commonly falcate, 2-5 times as long as broad, joined by acute or broad and rounded sinuses, the tips of most of them straight, or only slightly pointing toward the apex of the pinna (or penultimate segment), sterile margins apiculate-serrate (at least toward segment apex); venation copiously areolate, and with a single, long areole along the costa between midribs of adjacent ultimate segments; sori short to somewhat elongated, extending from the sinus $\frac{1}{4}$ - $\frac{3}{4}$ of the distance to the tip, rarely continuous around the sinus (but often appearing so); indusium whitish to gray, or yellowish brown, subentire to erose or (rarely) lacerate.

The name *P. propinqua*, so widely accepted for this species, must be abandoned in the place of *P. polita*, which has priority. The problem has been discussed in detail by Morton (Contr. U.S. Natl. Herb. 38: 75. 1967). Another name, *P. orizabae* Mart. & Gal. (Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 53. 1842) perhaps also should be included here. Although I have not examined the type, all specimens I have seen, so determined, do not differ significantly from *P. polita*.

In Guatemala, *P. polita* is likely to be confused with *P. podophylla*. The differences, though rather consistent, are generally subtle. These may be readily apparent if one has a number of specimens of both, for comparison, but the distinguishing features are less obvious to the collector who has not access to larger herbaria. One more characteristic may be helpful in delimiting the species. In *P. podophylla*, the costae of penultimate segments are provided with a number of castaneous, septate trichomes, these mostly borne within the channel, at least near the base of the segment. Costae are glabrous, adaxially, in *P. polita*.

***Pteris pungens* Willd. in L. Sp. Pl. 5: 387. 1810.**

In forests, frequently near swamps or along river banks, sea level to 600 m.; Alta Verapaz; Huehuetenango; Izabal; Petén. West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Bolivia.

Plants terrestrial; rhizome stout, erect or ascending, amply provided with linear scales, these 2-4 mm. long, amber to dark brown, most of them bicolorous with a narrow, blackish median stripe; leaves crowded, subcaespitose, to ca. 1.5 m. long, long-petiolate; petiole to ca. 90 cm. long, commonly much longer than the lamina, stout, terete, but flattened and usually broadly sulcate adaxially, yellowish to reddish brown, darkest at base, sparsely muricate or spinulose, essentially glabrous; lamina firm-herbaceous to chartaceous, glabrous, with 1-4 pairs of pinnae and a conform apical segment, essentially pinnate-pinnatisect, but the basal pair of pinnae 1-forked; rachis stramineous to light brown, sulcate adaxially, glabrous, smooth to sparsely muricate; pinnae sessile or subsessile, the basal pair forked, the branches unequal or subequal, each of them deeply pinnatisect, the other pinnae simple, deeply pinnatisect, gradually tapering at both ends, at the apex to a caudate terminal segment, toward the base the segments greatly reduced, the very basal ones often no more than broad auricles, adnate or decurrent along the costa; costae provided adaxially with short acute or subacute awns, one each at the base of an ultimate segment; ultimate segments linear or narrow-oblong, straight to slightly falcate, obtuse to subacute, serrate toward the apex; veins free, commonly 1-forked, 1 or 2 basiscopic ones arising from the costa, beneath the sinus (not from the segment midrib); sori elongated, often extending the length of the segment, from sinus to tip; indusium yellowish or greenish, entire.

***Pteris quadriaurita* Retz. Observ. Bot. 6: 38. 1791.**

In forests, thickets, and wooded ravines, often along banks of rivers and streams, occasionally on open roadside banks, 200-2,400 m.;

Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Escuintla; Guatemala; Huehuetenango; Quezaltenango; El Quiché; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Suchitepéquez; Zacapa. West Indies; Mexico to Colombia and Venezuela, south to Brazil and Bolivia; Old World tropics.

Plants terrestrial; rhizome stout, erect or ascending, provided with linear or linear-lanceolate scales, these 1-4 mm. long, commonly bicolorous, castaneous to blackish, with narrow, light-brown, erose to ciliate margins; leaves subcaespitose, to 2 m. long, petiolate; petiole to 1 m. long, about as long as the lamina, stout, terete abaxially, flattened to broadly sulcate adaxially, stramineous to light brown (or darker at base), glabrous, but with a few, scattered, linear, dark-brown scales at base; lamina firm-herbaceous to chartaceous, essentially glabrous, with 6-12 pairs of pinnae and a conform apical segment, essentially pinnate-pinnatisect, but the basal pair of pinnae 1-forked; rachis stramineous to yellow-brown, sulcate adaxially, glabrous, smooth; pinnae sessile to short-stalked, the basal pair forking, the branches unequal or subequal, each of them deeply pinnatisect, the other pinnae simple, deeply pinnatisect, tapered gradually to a caudate or subcaudate apex, scarcely or not at all reduced at base (if somewhat reduced then the basal segments commonly at least $\frac{1}{2}$ the length of the largest segments); costae provided adaxially with conspicuous, usually long-subulate awns, one each at or near the base of an ultimate segment; ultimate segments spreading at a broad (often 90°) angle from the costa, linear to narrow-oblong, straight or slightly falcate, obtuse to subacute, entire or (rarely) obscurely crenate, slightly and subequally (both acroscopically and basiscopically) broadening into the sinus, often bearing several conspicuous awns along the midrib adaxially; veins free, 1-2 mm. apart, commonly 1-forked, all arising from the midrib (or the basal basiscopic one occasionally borne on the costa near its juncture with the midrib); sori elongated, often extending the length of the segment from sinus nearly to tip; indusium yellow or yellow-brown, entire.

SACCOLOMA Kaulfuss

REFERENCE: R. Tryon, Taxonomic fern notes III: the genus *Saccoloma* Kaulf. Contr. Gray Herb. 141: 100-107. 1962.

Plants terrestrial, erect; rhizome scaly, erect or decumbent; leaves monomorphic, erect, crowded to fasciculate, essentially glabrous, or scaly at the petiole base; petiole not articulate; lamina pinnate (in 1 species) to decompose, commonly large and coarse, the axes sulcate adaxially, the ridges continuous with the basiscopic ridge of the axis of the next order above; veins free, simple or branched, terminating at or just short of the margins; sori submarginal, borne abaxially at the ends of veins, discrete (or in *S. elegans* contiguous and sometimes superficially appearing continuous along the margin); indusium obconic, attached to the vein at base and (at least partially) the sides, opening toward the margin, the segment or pinna margin slightly to strongly modified and functioning as the "back" of the indusium; paraphyses lacking; sporangia stalked; spores trilete, tetrahedral-globose, sharply ridged with perine.

There are about 10 species in this pantropical genus, with most occurring in the Old World. In the past these have been placed variously in *Orthiopteris* Copel. or *Ithycaulon* Copel., but Tryon (1962) has

shown that they are better combined under *Saccoloma*. All are rather large, coarse ferns of wet forests. Two quite distinct species occur in Guatemala.

- a. Leaves simply pinnate; sori contiguous and forming a nearly uninterrupted line along each pinna margin. *S. elegans*.
- a. Leaves 3- to 4-pinnate; sori discrete, borne on the tips of segments or lobes.
S. inaequale.

Saccoloma elegans Kaulf. Berlin Jahrb. Pharm. 51. 1820. *Davallia saccoloma* Spreng. Syst. Veg. 4: 119. 1827.

Apparently known from a single collection in Guatemala: Cubilguitz, Dept. Alta Verapaz, alt. 350 m., *Tuerckheim* (ed. Donn.-Sm. 7728); in forests, along marshes, or on stream banks, 0-350 m.; British Honduras; Nicaragua; Costa Rica; Panama; Greater Antilles; Trinidad; French and British Guiana; Venezuela; Colombia to Bolivia; Brazil.

Plants terrestrial; rhizome erect or decumbent, provided with lustrous, deep reddish brown scales, these lanceolate, to 5 mm. long, often obscured by a dense tangle of roots covered by copious orange to ferruginous root hairs; leaves pinnate, to 2 m. long and 0.6 m. broad; petiole to 60 cm. long, essentially glabrous, but near the base muricate or short-spiny, yellowish to reddish brown, usually darker at base, subterete abaxially, sulcate adaxially; lamina glabrous, chartaceous, ovate, terminating abruptly in a conform apical segment, scarcely reduced at base; rachis glabrous, yellow- to red-brown, sulcate adaxially, the marginal ridges continuous upward as the costal ridges of the pinnae; pinnae numerous, ascending, short-stalked to (distally) sessile, linear-lanceolate, cuneate at base, attenuate at apex, the margin serrulate to (especially at apex) sharply and deeply serrate, somewhat thinner textured and reflexed on fertile pinnae, the costa strongly prominulous and terete abaxially, narrowly sulcate adaxially; veins free, simple to 1-forked, 1.5-2 mm. apart, spreading from the costa at a broad angle, extending in subparallel fashion into the marginal serrations; sori numerous, contiguous, borne at tips of veins, forming a nearly uninterrupted line along the pinna margin from near the base to near the apex; indusium broad, half obconical, attached at its base (near the vein tip) and along its sides, open at the broad mouth, the slightly modified pinna margin forming an indusium-like "back" for the sorus.

Saccoloma inaequale (Kze.) Mett. Ann. Sci. Nat. Bot. IV. 15: 80. 1861. *Davallia inaequalis* Kze. Linnaea 9: 87. 1834. *Ithycaulon inaequale* (Kze.) Copel. Univ. Calif. Publ. Bot. 16: 80. 1929. *Orthiopteris inaequalis* (Kze.) Copel. Gen. Fil. 50. 1947.

In forests or wet, wooded ravines, 200-2,300 m.; Alta Verapaz; Baja Verapaz; Huehuetenango; San Marcos; Zacapa. Southern Mexico to Panama; West Indies; French Guiana to Colombia, south to Bolivia and Brazil.

Plants terrestrial; rhizome stout, erect, provided near the apex with lustrous, dark-brown scales, these linear or linear-lanceolate, attenuate, often twisted, to 7 mm. long; leaves to 2 m. long, crowded to fasciculate, 3- or 4-pinnate; petiole stout, about ½ the length of the lamina, essentially glabrous, or sparsely provided at base with dark-brown



FIG. 71. *Saccoloma*. a-b, *S. inaequale*: a, lamina, $\times \frac{1}{2}$; b, fertile pinnule, near apex, $\times 5$; c-d, *S. elegans*: c, silhouette of lamina, $\times \frac{1}{2}$; d, fertile pinna margin, $\times 5$.

scales, yellowish to reddish brown, usually darker at base, subterete abaxially, sulcate adaxially, lamina glabrous, chartaceous, ovate or deltoid-ovate, very gradually diminishing to a pinnatifid apex, scarcely reduced at base; rachis glabrous, drying stramineous to yellow- or gray-brown, this and other axes sulcate adaxially, the ridges continuous with the basiscopic ridge of the axis of the next order; pinnae ascending, stalked, ovate or deltoid-ovate, somewhat inequilateral at base, truncate acroscopically, cuneate and more strongly produced basiscopically, attenuate at apex, the pinnules anadromous; ultimate segments oblique, commonly obtuse, crowded, the sinuses between segments narrow and acute, lobed to serrate; veins several-forked to pinnately branched in the segments, terminating at or just short of the margin in the serrations; sori distant, 1 or several to a segment, borne at the ends of veins at the tips of segments or on 1 of the lateral lobes; indusium half obconical, attached at its base (near the vein tip) and along the sides, opening outward at a narrow mouth, the slightly modified margin of the lobe or segment forming an indusium-like "back" for the sorus.

SCHAFFNERIA Fée

Plants terrestrial or (more commonly) epipetric; rhizome compact, erect, provided with linear, gray-brown, clathrate scales 2-4 mm. long and 0.1-0.4 mm. broad; leaves simple, entire, erect, fasciculate, long- to short-petiolate, 2.5-8 cm. long; petiole not articulate, stout, 1-2 mm. thick, 0.5-6 cm. long, terete, lustrous, blackish (the color ending abruptly at the lamina base), scaly at base as on the rhizome, the scales becoming minute and hairlike distally; lamina entire, fleshy, orbicular or obovate-orbicular, sometimes as broad as or broader than long, midrib lacking, truncate or broadly cuneate at base, essentially glabrous; veins obscure, flabellate, several times forked, obliquely anastomosing (especially toward lamina margin); sori short to elongated (2-12 mm. long), borne along the veins throughout the lamina (except at the very base); indusium narrow, firm, attached along the vein, opening toward or away from the margin, single (asplenoid) or very rarely back-to-back (diplazoid); paraphyses lacking, sporangia stalked, glabrous; spores monolete, with perine.

Schaffneria is closely related to *Asplenium*, distinguished from the latter primarily by the areolate venation. The genus contains a single species.

Schaffneria nigripes Fée, Mém. Fam. Foug. 7: 56, t. 17. 1857. *Phyllitis nigripes* (Fée) O. Ktze. Rev. Gen. Pl. 2: 818. 1891. *Asplenium nigripes* (Fée) Hook. in Hooker's J. Bot. Kew Gard. Misc. 9: 268. 1857 (not Bl. 1860). *Scolopendrium nigripes* (Fée) Hook. Sp. Fil. 4: 3. 1862. *Antigramma nigripes* (Fée) J. Sm. Hist. Fil. 331. 1875.

In forests or thickets, commonly on rocks, 1,000-1,500 m.; Alta Verapaz; Chiquimula; Huehuetenango; Izabal (?). Southern Mexico; Costa Rica; Cuba.

Characters are those of the genus. Hemsley (Biol. Centr. Amer. 3: 641. 1885) reported a specimen from Izabal (*Godman & Salvin s.n.*), but I have not seen this.

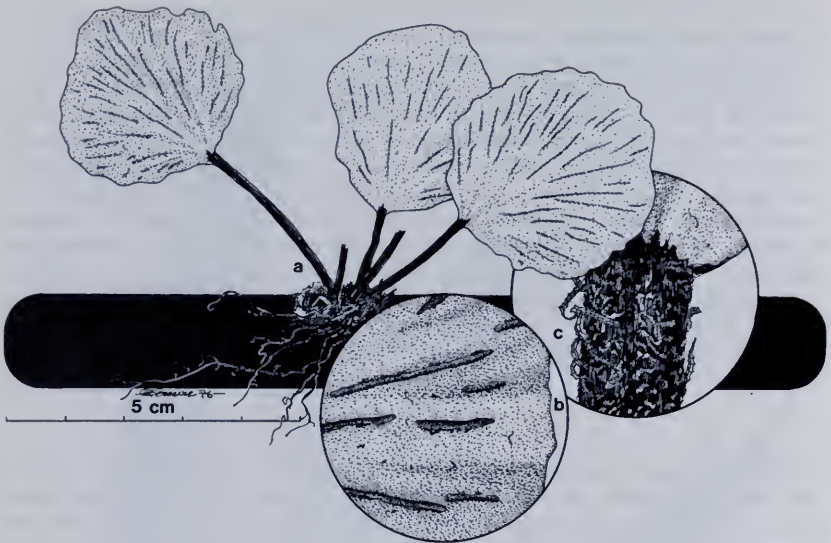


FIG. 72. *Schaffneria nigripes*. a, habit, $\times 1$; b, portion of fertile lamina, $\times 5$; c, petiole at base of lamina, $\times 12$.

STIGMATOPTERIS Christensen

REFERENCE: C. Christensen, On *Stigmatopteris*, a new genus of ferns. . . . Bot. Tidsskr. 29: 291-304. 1909.

Plants large, terrestrial, erect; rhizome stout, erect or ascending, scaly; leaves monomorphic, approximate to fasciculate, erect, the axes abaxially provided with brown, often fimbriate, scales, trichomes lacking; petiole not articulate; lamina pinnate to pinnate-pinnatisect (in ours) or 2-pinnate, glandular-punctate (often obscurely so), thin-herbaceous (in ours) to chartaceous, broadly lanceolate to subdeltoid, tapering to a pinnatifid apex; minor axes adaxially decurrent onto those of the next order below; pinnae commonly lanceolate or oblong-lanceolate, broadly serrate fully to the acuminate or attenuate apex; venation catadromous and free (in ours) or rarely areolate, the veins pinnate, terminating short of the margin, the tips enlarged; sori abaxial on the veins, round or occasionally somewhat elongated (in ours), or in 1 species confluent; indusium lacking (in ours) or in a few species peltate and glabrous; sporangia long-stalked; spores monolete, bilateral, with perine.

There are 20-25 species in this neotropical genus, many of them very closely related, if not conspecific. A number of species have been delimited chiefly on the degree of dissection of pinnae—an often unreliable feature when not combined with other characteristics. The following two species are found in Guatemala.

- a. Pinnae broadly serrate or deeply crenate (rarely shallowly lobed), all but the lower 3-4 pairs long-decurrent. *S. longicaudata*.

- a. Pinnae pinnatifid to deeply pinnatisect, only the uppermost pairs long-decurrent. . .
S. sordida.

Stigmatopteris longicaudata (Liebm.) C. Chr. Bot. Tidsskr. 29: 300. 1909. *Polypodium longicaudatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 209 (seors. 57). 1849. *Dryopteris longicaudata* (Liebm.) Maxon, Contr. U.S. Natl. Herb. 13: 18. 1909.

In dense, wet forests, often in ravines and along streams, 1,350-2,000 m.; Alta Verapaz; Baja Verapaz; Huehuetenango. Southern Mexico; Costa Rica; Panama.

Rhizome short, stout, erect or ascending, scaly; leaves to about 1.3 m. tall and 0.3 m. broad; petiole to 60 cm. long, smooth, provided with dark-brown, ovate to lanceolate, attenuate scales, sparsely so above, but often densely so at base; lamina glabrous, glandular-punctate, thin-herbaceous, pinnate or essentially so, ovate to subdeltoid, scarcely reduced at base, gradually tapering to a pinnatifid, often attenuate apex; rachis stramineous, provided with scattered, brown scales as on the petiole, abaxially rounded, adaxially canaliculate, the channel appearing minutely pubescent due to the presence of numerous stipitate glands; pinnae remote, ascending, lanceolate or oblong-lanceolate, to 20 cm. long and 2.5 cm. wide, the tips broadly serrate, attenuate, the margins broadly serrate to shallowly crenate (or very rarely obtusely lobed $\frac{1}{4}$ of the way to the costa), upper and middle ones fully adnate with the basiscopic base long-decurrent, lower ones free, often cuneate and short-stalked; costae provided abaxially with scattered brown scales; veins free, pinnate, terminating far short of the margin, the branches simple, curved-ascending, with enlarged, often clavate, tips; sori round, 1- to 3-seriate between costa and margin, abaxial on the branches of veins, borne at or near their tips; indusium lacking.

There is little to distinguish this from *S. rotundata* (Willd.) C. Chr. of Trinidad and the Lesser Antilles. Only the uppermost pinnae of the latter have long-decurrent bases, and some larger pinnae are lobed one-third to nearly halfway to the costa. Pinnae of *S. longicaudata* are either crenate or very shallowly lobed, and all but the lowermost have decurrent bases. If subsequent studies reveal no more significant differences than these, the two taxa will hardly merit more than infra-specific delimitation.

Stigmatopteris sordida (Maxon) C. Chr. Index Fil. Suppl. 3: 175. 1934. *Dryopteris sordida* Maxon, Contr. U.S. Natl. Herb. 24: 60. 1922.

In dense, wet forests, 250-350 m.; Alta Verapaz (type from forest near Cubilgüitz); Suchitepéquez. Mexico (Chiapas); Costa Rica.

Rhizome short, stout, erect or ascending, scaly; leaves to about 1.8 m. long and 0.6 m. broad; petiole to 80 cm. long, smooth, provided with dark-brown, ovate to lanceolate, usually attenuate scales, sparsely so above, but more densely so at base; lamina glabrous, glandular-punctate (often obscurely so), thin- to firm-herbaceous, pinnate-pinnatisect, ovate to subdeltoid, scarcely reduced at base, gradually tapering to a pin-



FIG. 73. *Stigmatopteris*. a-b, *S. longicaudata*: a, habit, $\times \frac{1}{2}$; b, rachis and pinna bases, $\times 4$; c, *S. sordida*, pinna, $\times \frac{1}{2}$.

natifid, often attenuate apex; rachis stramineous, provided with scattered brown scales as on the petiole, abaxially rounded, adaxially canaliculate, the channel appearing minutely pubescent due to the presence of numerous stipitate glands; pinnae remote, spreading to ascending, lanceolate or oblong-lanceolate, to 30 cm. long and 6 cm. wide, the tips broadly serrate, attenuate, the distal ones deeply crenate to lobed and fully adnate, the others cut two-thirds or almost fully to the costa, and free and short-stalked; veins free, pinnate, terminating far short of the margin, the branches simple or 1-forked, with enlarged, often clavate tips; sori round or (rarely) somewhat elongate, 4-11 pairs per segment, abaxial on the veins, borne about midway along the simple ones or at the fork of branched ones; indusium lacking.

The species varies somewhat as to the degree of dissection of pinnae. On smaller specimens, pinnae may be cut halfway to three-fourths to the costa, with the segments relatively broad; but on larger leaves the pinnae are sometimes cut nearly to the costa, appearing subpectinate, with segments very long and narrow. The largest, most deeply dissected, specimens very closely resemble *S. pellucidopunctata* C. Chr. of Peru, at least superficially. I have not seen the type, but a photograph of the isotype at British Museum is remarkably similar to larger specimens of *S. sordida*. However, Christensen's illustration of segments of the type (Bot. Tidsskr. 29: 304, t. 15. 1909) shows sori borne well out on a vein branch, whereas sori of *S. sordida* are borne at the fork, on branched veins. Further comparison of the two species would be desirable in order to clarify relationship.

TECTARIA Cavanilles

REFERENCE: C. V. Morton, The Mexican species of *Tectaria*, Amer. Fern J. 56: 120-137. 1966.

Plants terrestrial; rhizome creeping, or ascending to erect, scaly; leaves monomorphic, long-petiolate, subdistant to crowded or fasciculate; petiole not articulate, scaly at base (or sometimes throughout), and commonly pilosulous adaxially with short, septate trichomes; lamina simple to coarsely decompound, papyraceous to chartaceous, the tissue glabrous or (occasionally) minutely pubescent, the axes commonly short-pubescent at least on the adaxial side, proliferous buds sometimes borne along or at the tip of the rachis or at the bases of pinnae; rachis commonly sulcate adaxially, rarely scaly, but often minutely pilosulous in the adaxial groove; pinnae (if any) commonly short-stalked, the basal ones frequently asymmetrical, with 1 to several conspicuous basiscopic lobes; venation reticulate, the areoles commonly with included free veinlets, these with tips spreading in various directions; sori abaxial on the veins or at the tips of veinlets, round (or rarely elongated due to the merging of adjacent ones); indusium peltate or circular-reniform or lacking; paraphyses lacking; sporangium long-stalked; spores monolete, with perine, commonly tuberculate or spinulose.

More than 200 species have been recognized around the world, these occurring in wet tropical (rarely subtropical) regions. Realistically, the number should be much less, for many species are being reduced to

synonymy, and several segregate genera have been recognized. Probably less than 40 occur in the neotropics, six of these in Guatemala.

- a. Leaves simple, not lobed. *T. plantaginea*.
- a. Leaves lobed to decompose.
 - b. Leaves (at least toward the base) 2-pinnate or more.
 - c. Free, included veinlets common in the areoles; rhizome scales glabrous; leaves 2-pinnate to 2-pinnate-pinnatifid; alt. 30-350 m. *T. rheosora*.
 - c. Free, included veinlets rare or lacking in the areoles; rhizome scales pilosulous; leaves 2-pinnate-pinnatifid to 3-pinnate-pinnatifid; alt. 250-1,800 m. *T. mexicana*.
 - b. Leaves pinnatifid to pinnate-pinnatifid.
 - d. Leaves pinnatifid, the rachis alate throughout; rhizome creeping, the leaves subdistant; basal pinnae (segments) the smallest. *T. nicotianifolia*.
 - d. Leaves pinnate (or young leaves nearly 3-foliolate in *T. heracleifolia*), the rachis mostly free; rhizome suberect, the leaves crowded to caespitose; basal pinnae (segments) the largest.
 - e. Indusium reniform (often appearing circular), attached at a deep, proximal sinus; pinnae of mature leaves (2) 4-10 pairs; apical section and first pair of pinnae conspicuously decurrent on rachis [*T. incisa*].
 - f. Lower (and often middle) pinnae with several conspicuous basiscopic lobes; lamina minutely but amply pubescent on abaxial side; alt. 900-1,600 m. ... *T. incisa* ssp. *transiens*.
 - f. Lower pinnae with a single conspicuous basiscopic lobe; lamina essentially glabrous; alt. 0-900 m.
 - g. Lamina lacking proliferous buds. *T. incisa* var. *incisa*.
 - g. Lamina adaxially with 1 to several proliferous buds borne usually at pinna bases. *T. incisa* f. *vivipara*.
 - e. Indusium peltate, circular, centrally attached; pinnae of mature leaves (if any) 1-2 (3) pairs; apical section rounded to cordate at base (rarely decurrent, and then the first pair of pinnae cordate and usually stalked) [*T. heracleifolia*].
 - h. Lamina glabrous. *T. heracleifolia* var. *heracleifolia*.
 - h. Lamina with both surfaces and margins conspicuously hirsute. *T. heracleifolia* var. *trichodes*.

***Tectaria heracleifolia* (Willd.) Underw. Bull. Torrey Bot. Club 33: 200. 1906.**

Plants terrestrial, often epipetric; rhizome erect or ascending; amply provided with linear to lanceolate scales, these dark brown to blackish, often with lighter colored margins, entire or occasionally denticulate to short-fimbriate, 2-5 mm. long; leaves to 1.2 m. long and 0.25 m. broad, subcaespitose; petiole to 70 cm. long, commonly longer than the lamina, stramineous to reddish brown, terete to angular abaxially, sulcate adaxially, sparsely scaly near the base; lamina simple to 3-foliolate, or pinnate, papyraceous, glabrous, (hirsute in var. *trichodes*), deltoid-ovate, the apex acuminate, the base cordate, the free apical section (if any) rounded to cordate (very rarely decurrent, and then the first pair of pinnae cordate and usually stalked); rachis commonly stramineous, not gemmiferous; pinnae (if any) of mature leaves 1-2 (3) pairs, deltoid, stalked, acuminate, entire to sinuate or deeply and broadly crenate, commonly with a strongly produced basiscopic lobe, basal pinnae the largest; venation reticulate, with numerous included,



FIG. 74. *Tectaria*. a, *T. nicotianifolia*, habit, silhouette, $\times \frac{1}{2}$; b, *T. plantaginea*, habit, $\times \frac{1}{2}$; c-d, *T. mexicana*: c, pinna, $\times \frac{1}{2}$; d, portion of larger pinnule, showing venation, $\times 7\frac{1}{2}$; e, *T. rheosora*, venation and indusia, $\times 7\frac{1}{2}$; f, *T. heracleifolia* var. *heracleifolia*, venation and indusia, $\times 7\frac{1}{2}$.

free veinlets, commonly a single costal areole between the primary veins; sori round, borne in 1 row along either side of the primary vein; indusium subpersistent, circular, peltate.

Specimens of *T. heracleifolia* with more than one pair of pinnae can be confused with *T. incisa*, especially those with very mature leaves, whose indusia are so greatly contracted that the presence or absence of a sinus is not determinable. The free apical section of *T. incisa* and at least the first pair of pinnae are conspicuously decurrent on the rachis. However, in pinnate specimens of *T. heracleifolia* the free apical section is commonly cordate, or broadly rounded. Very rarely it may be decurrent, but in this case, the first pair of pinnae are cordate and usually stalked.

Several varieties of *T. heracleifolia* have been proposed. Of these, var. *heracleifolia* and var. *trichodes* occur in Guatemala.

***Tectaria heracleifolia* var. *heracleifolia*.** *Aspidium heracleifolium* Willd. in L. Sp. Pl. ed. 4, 5: 217. 1810. *Bathmium heracleifolium* (Willd.) Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 287. 1852. *A. trifoliatum* ssp. *heracleifolium* Clute, Fern Bull. 16: 82. 1908. *T. trifoliata* var. *heracleifolia* Farw. Amer. Mid. Naturalist 12: 261. 1931. *T. trifoliata sensu* Millsp. Publ. Field Columb. Mus., Bot. Ser. 3: 3. 1903 (not Cav. 1802).

In forests or thickets, in ravines, or along stream banks, often on rocks or on limestone bluffs, 0-1,500 m.; Alta Verapaz; Huehuetenango; Izabal; Petén; El Quiché; Santa Rosa; Zacapa. Florida; West Indies; Mexico to Peru.

Leaves simple to 3-foliolate, or pinnate with 1-2 (3) pairs of pinnae, mature ones 20-110 cm. long; petiole to 70 cm. long; lamina glabrous.

Tectaria heracleifolia* var. *trichodes Morton, Amer. Fern J. 56: 126. 1966.

On rocks or limestone cliffs, 300-900 m.; Alta Verapaz (type from Cerro de Agua Tortuga, near Cubilguitz, *Steyermark 44586*).

Leaf simple or 3-foliolate, 12-40 cm. long; petiole to 25 cm. long; lamina with both surfaces and margins conspicuously hirsute.

Tectaria incisa Cav. Descr. Pl. 249. 1802.

Plants terrestrial; rhizome erect, amply provided with lanceolate or ovate scales, these castaneous to blackish, often with lighter colored, short-fimbriate margins, 3-7 mm. long; leaves to 1.3 m. long and 0.4 m. broad, subcaespitose; petiole to 90 cm. long, equaling or much longer than the lamina, stramineous to reddish brown, terete to angular abaxially, sulcate and minutely puberulous adaxially, sparsely scaly near the base; lamina pinnate, papyraceous to firm-herbaceous, glabrous, or minutely pubescent on 1 or both sides, oblong or ovate-oblong, the apex acuminate, the free apical section

and at least the first pair of pinnae conspicuously decurrent on the rachis; rachis yellowish to reddish brown, free except at the apex, not gemmiferous, or (in f. *vivipara*) bearing proliferous buds at the pinna bases adaxially; pinnae of mature leaves (2) 4-10 pairs, lanceolate to elliptic, short-stalked or (toward the apex) adnate to decurrent, acuminate, entire to shallowly lobed, or the basal (and rarely the lower middle) pairs with 1 or 2 very strongly produced basiscopic lobes, basal pinnae the largest; venation reticulate, with numerous included, free veinlets; sori round, borne in 1 row along either side of the primary vein; indusium subpersistent, appearing circular, but actually reniform, attached at a deep, proximal sinus.

This is one of the most highly variable of the species of *Tectaria*, as witnessed by the numerous infraspecific taxa into which it has been subdivided. Whether or not the status of each subspecies, variety, or form has been correctly assessed is conjectural at this point, and the entire problem should be reappraised in future monographic study. For taxa which occur in Guatemala, Morton's categories have been retained for purposes of the present treatment.

Several aberrant specimens of *T. subincisa* have been collected in the departments of Escuintla, Izabal, and San Marcos, as well as in Honduras. These resemble the typical variety in most respects, but some of the pinnae, and sometimes the apical sections, have a number of deep, narrow lobes. In some cases the lobes are so narrow and attenuate that the pinnae are almost lacinate. In all these specimens the sporangia or spores appear to be abortive, suggesting a hybrid origin.

Tectaria incisa may be confused with plants of *T. heracleifolia* which have more than one pair of pinnae. See discussion of the latter for further information.

***Tectaria incisa* var. *incisa*.** *Aspidium martinicense* Sprengel, Anleit. Kenntn. Gewächse 3: 133. 1804. *A. macrophyllum* Rud. Bemerk. Geb. Naturg. 2: 103. 1805 (nom. illeg.). *Palma negra* (fide Steyermark, Suchitepéquez).

Terrestrial, in wet forests, often on slopes or in shaded ravines, 0-900 m.; Alta Verapaz; Baja Verapaz; Escuintla; Izabal; Petén; San Marcos; Santa Rosa; Suchitepéquez. West Indies; Mexico to Panama, south to Bolivia and Brazil. Escaped from cultivation and apparently naturalized in southern Florida.

Basal pinnae with a single, conspicuous basiscopic lobe; lamina glabrous (or the axes and margins sparsely and minutely pubescent).

***Tectaria incisa* forma *vivipara* (Jenm.) Morton,** Amer. Fern J. 56: 131. 1966. *Nephrodium macrophyllum* var. *viviparum* Jenm. Bull. Bot. Dept. Jamaica, n.s. 3: 238. 1896. *Aspidium macrophyllum* var.

biolleyanum Christ in Pittier, Prim. Fl. Costaric. 3: 30. 1901. *T. martinicensis* var. *vivipara* Domin, Rozpr. Král. České Společn. Nauk., Tr. Mat.-Prir. 2: 231. 1929.

Terrestrial, in forest, 0-350 m.; Alta Verapaz; Petén. Jamaica; Mexico; Nicaragua to Colombia; Brazil.

This differs from var. *incisa* only in the presence of 1 to several proliferous buds on the adaxial side of the lamina, these borne usually at the bases of pinnae.

***Tectaria incisa* ssp. *transiens* Morton, Amer. Fern J. 56: 133. 1966.**

Terrestrial, in wet forests, often on slopes or in ravines, 900-1,600 m.; Alta Verapaz; Huehuetenango; Suchitepéquez. Southern Mexico (type from Córdoba, Veracruz, *Hugo Finck* 57); Nicaragua; Costa Rica.

Basal (and sometimes middle) pinnae with 2 or more conspicuous basiscopic lobes; lamina minutely but amply pubescent on abaxial side.

***Tectaria mexicana* (Fée) Morton, Amer. Fern J. 56: 133. 1966.**
Sagenia mexicana Fée, Mém. Fam. Foug. 5 (Gen. Fil.): 313. 1852.
Aspidium cicutarium sensu auctt. (not *Polypodium cicutarium* L. 1759). *T. dilacerata sensu auctt.* (not *Aspidium dilaceratum* Kunze 1850).

In forests, thickets, or shaded ravines, often along streams and rivers, 250-1,800 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Quezaltenango; Retalhuleu; Sacatepéquez; San Marcos; Santa Rosa; Suchitepéquez. Mexico to Colombia.

Plants terrestrial; rhizome creeping or obliquely ascending, amply provided with brown, minutely ciliate, pilosulous scales, these somewhat lustrous, with elongated, thickened cells; leaves 0.5-1 m. long and 0.3-0.5 m. broad, crowded at the rhizome tip; petiole 20-50 cm. long, somewhat shorter or nearly equaling the lamina, light or dark brown, subterete abaxially, bisulcate adaxially, minutely pilose with septate trichomes, scaly at base as on the rhizome; lamina 2-pinnate-pinnatifid to 3-pinnate-pinnatifid, firm-membranaceous or herbaceous, deltoid, tapering gradually to a pinnatifid apex, not gemmiferous, the axes, veins and margins pilosulous with minute, septate trichomes, tissue between the veins glabrous, or adaxially with a single, septate trichome in some of the areoles or rarely (outside of Guatemala) both sides pilosulous within the areoles; rachis dark or yellowish brown, densely pubescent to glabrate, free except at the apex; pinnae ascending, subopposite, acuminate, distal ones sessile or adnate, medial and proximal ones stalked (to 4 cm.), lanceolate to ovate, pinnatifid to 2-pinnate-pinnatifid, with pinnules or segments catadromous, basal pinnae subdeltoid, basiscopically enlarged, their pinnules anadromous; venation reticulate, included free veinlets few or lacking, costal areoles between primary veins 2, the distal one running out along the costule; sori round, borne commonly in 1 row between midrib and segment margin; indusium persistent, circular, with a deep, narrow sinus and overlapping lobes, thus pseudopeltate.

Morton (1966) described var. *pilosula* based on some Mexican specimens which have numerous trichomes within each areole, on both surfaces. Although my studies have revealed more of these pilosulous specimens scattered throughout southern Central America, I have observed none in Guatemala.

There has been much confusion in the determination of plants of this species, with the result that numerous specimens may be found currently in herbaria identified as *T. cicutarium* or *T. dilacerata*, *Aspidium cicutarium* or *Nephrodium cicutarium*. For clarification of the taxonomic and nomenclatural problems, see Morton's excellent treatment of the Mexican species (*loc. cit.*).

Tectaria nicotianifolia (Bak.) C. Chr. Index Fil. Suppl. 3: 182. 1934. *Polypodium nicotianifolium* Bak. in Hook. & Bak. Syn. Fil. 455. 1868. *Aspidium nicotianifolium* (Bak.) Diels, Nat. Pflanz. 1 (4). 1899. *A. eurylobum* Christ, Bull. Soc. Roy. Bot. Belgique 35: 206. 1896. *T. euryloba* (Christ) Maxon, Amer. Fern J. 17: 6. 1927.

In deep forests, usually along stream banks or in ravines, 50-400 m.; Izabal; Suchitepéquez. Honduras; Nicaragua to Colombia and Ecuador.

Plants terrestrial; rhizome creeping, amply provided with brown, appressed, ovate or lanceolate, entire scales intermixed with lustrous, tortuous, filiform trichomes; leaves to 1 m. long and 0.3 m. broad, subdistant; petiole to 50 cm. long, equaling or shorter than the lamina, yellowish to reddish brown, terete to subquadrangular abaxially, bisulcate adaxially, densely pilosulous to glabrate, and amply provided with spreading, lustrous, lanceolate or linear, entire scales, these commonly as abundant at the apex as near the base; lamina deeply pinnatifid, very broadly alate throughout, thin-herbaceous, oblong-deltoid, terminal segment to 30 cm. long and 10 cm. broad, larger than the lateral ones (ca. 15-25 cm. long and 6-7 cm. broad); segments entire or very broadly sinuate, acuminate, subdistant, ascending from acute to (more commonly) broadly rounded or truncate sinuses, basal segments much the smallest; venation copiously reticulate, with numerous included, free veinlets, primary veins ca. 8-12 mm. apart, distinct nearly to the segment margin, secondary veins commonly distinct, scarcely raised; sori small, round (or sometimes merging and thus elongated), commonly borne on the tips of free veinlets, in 6-10 very irregular rows between primary veins; indusia lacking.

Tectaria nicotianifolia is readily distinguished by its simply pinnatifid lamina and the rachis which is very broadly alate throughout. It is very similar to *T. myriosora* (Christ) C. Chr. of southern Central America and *T. draconoptera* (Eat.) Copel. of northern South America and, in fact, future study may eventually reveal the three to be conspecific.

Tectaria plantaginea (Jacq.) Maxon, Contr. U.S. Natl. Herb. 10: 494. 1908. *Polypodium plantagineum* Jacq. Coll. Bot. 2: 104. 1788.

Aspidium plantagineum (Jacq.) Griseb. Abh. Königl. Ges. Wiss. Göttingen 7: 268. 1857.

Not yet reported from Guatemala, but to be expected here. In deep, wet forests, along streams and in ravines, often on rocks in streams, 30-600 m.; British Honduras; Honduras south to Peru and Brazil; West Indies.

Plants terrestrial; rhizome creeping, provided with ovate to lanceolate, brown, entire scales, trichomes lacking; leaves simple, erect, crowded, 25-45 cm. long, 4-12 cm. broad; petiole 4-12 (20) cm. long, much shorter than the lamina, amply provided with light- to dark-brown, lanceolate, attenuate scales; lamina entire or weakly and broadly sinuate, herbaceous, oblong or oblanceolate, the apex commonly obtuse, often emarginate and proliferous, the base strongly decurrent, the tissue glabrous or the abaxial surface very sparsely provided with minute hairlike scales; costa dark brown, adaxially sulcate, abaxially subterete and strongly raised, scaly and often minutely pilosulous; primary veins ascending, 0.7-1 cm. apart, dark colored, conspicuous and (sometimes) minutely pilosulous abaxially, strongly or weakly sinuate, bearing between them several series of areoles, these commonly with a free, included veinlet; sori round or elongated, borne on secondary veins in a regular row along each side of a primary vein; indusium lacking.

The simple leaf of *T. plantaginea* can hardly be confused with any other Guatemalan species. *Tectaria nicaraguensis* (Fourn.) C. Chr. of southern Central America is similar, but the leaf apex is acuminate, and the base of the lamina is truncate or cordate.

Tectaria rheosora (Bak.) C. Chr. Index Fil. Suppl. 3: 184. 1934.
Polypodium rheosorum Bak. J. Bot. 363. 1884 (not Baker, 1891).
Aspidium rheosorum (Bak.) C. Chr. Index Fil. 90. 1905.

In deep forests, often along streams or in ravine bottoms, 30-350 m.; Alta Verapaz; Izabal. British Honduras; Nicaragua; Costa Rica; Panama.

Plants terrestrial; rhizome stout, woody, ascending, amply provided with glabrous, thickened, somewhat bicolorous scales, these lustrous and dark brown or blackish, with dull, lighter brown, erose margins; leaves to 1.5 m. long and 0.5 m. broad, crowded on the rhizome apex; petiole to 80 cm. long, equaling or slightly shorter than the lamina, reddish brown, terete abaxially, bisulcate adaxially, minutely pilose, sparsely appressed-scaly at base; lamina pinnate-pinnatifid to 2-pinnate-pinnatifid, firm-herbaceous, deltoid, tapering gradually to a pinnatifid apex, not gemmiferous, the axes, veins, and margins pilosulous with minute, septate trichomes, the tissue between veins glabrous; rachis reddish brown, densely pubescent to glabrate, free except near the apex; pinnae ascending, subopposite, acuminate, distal ones subsessile or adnate, medial and proximal ones long-stalked (to 6 cm.) lanceolate to ovate, pinnatifid to pinnate-pinnatifid, with segments catadromous, basal pinnae subdeltoid, basiscopically enlarged, their pinnules commonly anadromous; venation reticulate, with numerous included free veinlets, costal areoles between primary veins 1-2; sori round, or elongated due to merging of adjacent ones, borne in 1-3 rows between midrib and segment margin; indusium subpersistent, circular, with a deep, narrow sinus and often-overlapping lobes, thus pseudopeltate.

THELYPTERIS Schmidel

ALAN R. SMITH

University of California, Berkeley

REFERENCES: C. Christensen, Revision of the American species of *Dryopteris* of the group of *D. opposita*, Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 4: 247-336. 1907. C. Christensen, A monograph of the genus *Dryopteris*. Part I. The tropical American pinnatifid-bipinnatifid species, Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 55-282. 1913. W. R. Maxon and C. V. Morton, The American species of *Dryopteris*, subgenus *Meniscium*, Bull. Torrey Bot. Club 65: 347-376. 1938. A. R. Smith, Systematics of the neotropical species of *Thelypteris* section *Cyclosorus*, Univ. Calif. Publ. Bot. 59: 1-136. 1971. A. R. Smith, The Mexican species of *Thelypteris*, subgenera *Amauropelta* and *Goniopteris*, Amer. Fern J. 63: 116-127. 1973.

Habitat terrestrial to rarely epipetric; rhizomes long-creeping to short-creeping to erect, dictyostelic, scaly, the scales entire and usually ciliate on the margin and/or surface; stipes in cross section with 2 crescent-shaped vascular bundles at the base, these fusing distally; stipes, rachises, and costae adaxially sulcate, the sulci not running continuously into the axis of the next order; fronds simple to pinnate to usually pinnate-pinnatifid, to decompound (Old World groups); laminae, stipes, and/or rachises nearly always at least sparingly hairy, the hairs acicular (unicellular or multicellular), hamate, or stellate; sori dorsal on the veins, occasionally submarginal, with or without reniform indusia; spores bilateral, monolete (tetrahedral and trilete in a few Old World species), with a usually prominent perispore; gametophyte cordate, superficial, usually glandular or hairy; $x = 36, 35, 34, 32, 31, 30, 29, 27$.

In its broadest sense as taken here, *Thelypteris* is a genus of about 1,000 species, distributed pantropically, with a few species in temperate areas. There are perhaps 300 species in the neotropics, 58 in Guatemala. *Thelypteris sensu lato* has been subdivided by many pteridologists into natural groups variously treated as genera, subgenera, or sections. I believe that most of these can be well circumscribed using several characters, and thus could stand as genera. However, largely as a matter of convenience, I prefer to maintain an inclusive genus with several subgenera. Those subgenera occurring in Guatemala can be distinguished by the following key:

- a. At least some of the hairs on the rachis, costae, stipe base, and/or stipe base scales forked or stellate. subg. GONIOPTERIS. p. 495
- a. Hairs all acicular, unicellular or multicellular.
 - b. Lamina essentially pinnate, the pinnae entire or with an undulate or serrate margin, occasionally very shallowly lobed; areoles formed by the united or meniscioid veins, 3-15 seriate.

- c. Sori mostly discrete, or only the basal pair confluent.
subg. GONIOPTERIS. p. 495
- c. Sori mostly confluent where the veins anastomose. subg. MENISCIUM. p. 508
- b. Lamina pinnate-pinnatifid $\frac{1}{2}$ or more to the costae, 2-pinnate in 1 species; veins free, connivent at the sinus, or with 1-2 pair(s) anastomosing.
d. Laminae 2-pinnate-pinnatifid or more divided.
subg. MACROTHELYPTERIS. p. 507
- d. Laminae 1-pinnate-pinnatifid.
 - e. Lamina reduced toward the base, with 1 or usually several pairs of reduced pinnae, the lowermost pinnae often auriculiform or glanduliform; veins free, meeting the margin above the sinus (at the sinus in *T. linkiana*).
subg. AMAUROPOLTA. p. 474
 - e. Lamina without reduced pinnae, the lowest the longest or nearly the longest; veins connivent at the sinus or meeting the margin at the sinus, or if greatly reduced pinnae are present the veins anastomosing with an excurrent vein to the sinus.
 - f. Sori elongate along the veins, exindusiate, sporangial walls often setose.
subg. STEGNOGRAMMA. p. 511
 - f. Sori round, indusium present and persistent (absent in subg. *Steiropteris*), sporangial walls without setae.
 - g. Indusia present and persistent, large; aerophores at base of pinnae inconspicuous or absent. subg. CYCLOSORUS. p. 487
 - g. Indusia absent; aerophores 2-10 mm. long at base of pinnae.
subg. STEIROPTERIS. p. 512

THELYPTERIS subg. **AMAUROPOLTA** (Kunze) A. R. Smith, Amer. Fern J. 63: 121. 1973. *Amauropelta* Kunze, Farrnkr. 1: 86, 109. 1843.

Rhizomes suberect to erect, occasionally decumbent; laminae pinnate-pinnatifid (rarely pinnate or decompound), with the lowermost pinnae reduced, sometimes nearly to the rhizome; aerophores present at bases of pinnae, or absent; veins usually simple, occasionally furcate, the lowermost of a segment meeting the margin above the sinus; sori round to occasionally somewhat elongate, medial to submarginal on the veins, furnished with large to small indusia, or indusia absent; sporoderm evenly granular (light microscope), finely reticulate (scanning electron microscope); $x = 29$.

About 200 species, mostly at middle to higher elevations on margins of rain forests, along trails, wet roadside embankments, and margins of streams; tropical and subtropical America (Florida, Mexico, Antilles, Central America, and South America to northern Argentina and Chile), with one species in Hawaii and a few in Africa, Madagascar, and the Mascarene Islands (Smith, Amer. Fern J. 64: 83-95. 1974; Holttum, J. South African Bot. 40: 123-168. 1974).

- a. Indusia absent, or minute and completely obscured by sessile glands.
- b. Sori oblong or elongate along the veins.
- c. Lowermost veins meeting the margin at or near the sinus; leaf tissue below

- glabrous or very sparsely hairy; pinnae incised to ca. 2 mm. from costae.
T. linkiana.
- c. Lowermost veins meeting the margin above the sinus; leaf tissue below with hamate hairs; pinnae incised to within 1 mm. of costae. *T. atrovirens.*
- b. Sori round or nearly so.
- d. Hairs fasciculate or subfasciculate on costae and rachis below, appearing stellate; red or orange hemispherical glands present on leaf tissue below; aerophores at base of costae up to 4 mm. long.
- e. Hairs fasciculate; aerophores present at base of costules; pinnae greater than 2 cm. broad. *T. thomsonii.*
- e. Hairs subfasciculate; aerophores absent at base of costules; pinnae less than 2 cm. broad. *T. nubigena.*
- d. Hairs not fasciculate and not appearing stellate; glands absent; costal aerophores absent or less than 1 mm. long.
- f. Sporangia setulose; costae and rachis below minutely puberulous, the hairs much less than 0.1 mm. long. *T. concinna.*
- f. Sporangia glabrous; costae and rachis below not minutely puberulous.
- g. Costae below with at least a few scales, especially near the base, the scales \pm clathrate.
- h. Fronds small, less than 50 (70) cm. long, 8 (12) cm. broad; reduced basal pinnae 2-3 pairs; veins 5-7 pairs per segment; leaf tissue glabrous below. *T. caucaensis.*
- h. Fronds usually greater than 70 cm. long, 12 cm. broad; reduced basal pinnae 5-12 pairs; veins usually more than 7 pairs per segment; leaf tissue below pubescent or glabrous.
- i. Hairs on costae below more or less antrorse, mostly less than 0.6 mm. long; receptacular tissue glabrous or with a few short hairs; segments somewhat oblique, rounded or acute at tip. *T. rudis.*
- i. Hairs on costae below mostly erect, up to 1.5 mm. long; receptacular tissue with stiff hairs like those of costae; segments \pm perpendicular to costae, rounded at the tip. *T. piloso-hispida.*
- g. Costae below without scales.
- j. Rachis rather densely short-hairy; stiff hairs on costules and veins above. *T. oligocarpa.*
- j. Rachis glabrous; costules and veins above glabrous. *T. deflexa.*
- a. Indusia present, usually not obscured by glands.
- k. Hairs fasciculate or subfasciculate on costae and rachis below; red or orange hemispherical glands on leaf tissue below; aerophores present at base of costae.
see couplet (e).
- k. Hairs hamate or acicular, not fasciculate; hemispherical glands present or absent; aerophores present or absent at base of costae.
- l. Hamate hairs present on leaf tissue below and/or indusia; glands absent on leaf tissue.
- m. Reduced pinnae usually 2-4 pairs; rachis often darkened, densely hairy, the hairs 0.1-0.2 mm. long with a few longer ones intermixed; indusium tan. ...
T. oligocarpa.
- m. Reduced pinnae more than 5 pairs, nearly to the base of the frond; rachis stramineous, not densely hairy.
- n. Indusia dark-castaneous to blackish. *T. melanochlaena.*
- n. Indusia stramineous to tan. *T. scalaris.*

- l. Hamate hairs absent on leaf tissue and indusia; glands present or absent on leaf tissue.
 - o. Stipe and rachis hairs stiff, numerous, mostly 1-1.5 mm. long.
 - p. Sori submarginal, often partially hidden by the revolute leaf margin; costal and rachis hairs septate; veins immersed below, often darkened; basal basiscopic segment of well-developed pinnae longer than the others, parallel to rachis. *T. cheilanthoides*.
 - p. Sori medial to supramedial, not hidden by the margin; hairs mostly unicellular (not septate); veins not immersed below, usually slightly raised, stramineous; basal segments of pinnae not enlarged or elongate.
 - q. Indusia rather large; costules and veins above with stout, stiff hairs to 1 mm. long. *T. pilosula*.
 - q. Indusia small, inconspicuous; costules and veins above glabrous. *T. cheilanthoides*.
 - o. Stipe and rachis hairs mostly less than 0.3 mm. long, or, if longer, flexuous.
 - r. Fronds small, mostly less than 40 cm. long, with stipes 1-1.5 mm. in diameter; reduced basal pinnae 1-4 pairs; rachises glabrous or minutely puberulous.
 - s. Rachis and stipes usually darkened; rachis puberulous with hairs less than 0.1 mm. long; indusia reddish brown. *T. cinerea*.
 - s. Rachis and stipes stramineous, \pm glabrous; indusia tan. *T. sancta*.
 - r. Fronds usually large, greater than 40 cm. long, with stipes more than 2 mm. in diameter; reduced basal pinnae 5 or more pairs.
 - t. Rachis, costae, veins, and leaf tissue below without hairs or glands (occasionally with obscure glands).
 - u. Segments oblong, not falcate, rounded at tip; indusia rather large, persistent; pinnae incised to ca. 1 mm. from costae. *T. oaxacana*.
 - u. Segments linear to lanceolate, acutish at tip, subfalcate; indusia relatively small, somewhat obscured in mature sori; pinnae incised to within 0.5 mm. of costae. *T. struthiopteroides*.
 - t. Rachis, costae, veins, and leaf tissue below sparsely to densely hairy; glands usually present on leaf tissue below.
 - v. Sori submarginal, often partially hidden by the revolute leaf margin; usually a few long-septate hairs on costae and rachis below; veins immersed below, often darkened; glands absent from leaf tissue below. *T. cheilanthoides*.
 - v. Sori medial to submarginal, usually not hidden by segment margin; septate hairs usually absent; veins slightly raised below, not darkened; sessile, hemispherical glands present or absent on leaf tissue below.
 - w. Pinna segments oblique, usually falcate; pinnae gradually reduced nearly to the base of frond; pinna segments mostly 2-3 times as long as broad. *T. resinifera*.
 - w. Pinna segments \pm perpendicular to costae, occasionally oblique; pinnae usually abruptly reduced below, with widely spaced smaller pinnae; segments mostly 4-6 times longer than wide. *T. balbisii*.

Thelypteris atrovirens (C. Chr.) Reed, *Phytologia* 17: 261. 1968.
Dryopteris atrovirens C. Chr. in Christ, *Bull. Herb. Boissier* II. 7: 263. 1907.

Uncommon, along streams in dense forest, 200-1,200 m.; Alta Verapaz (type from between Sepacuité and Secanquim, *Maxon & Hay 3281*, P; isotypes NY! US!); Huehuetenango; Izabal. Southern Mexico; Nicaragua; Costa Rica; Panama.

Rhizomes erect; fronds fasciculate, up to 80 cm. long, with 7-10 pairs of gradually reduced basal pinnae; stipes 5-15 cm. long, scaly at the base; pinnae 20-30 pairs, horizontal, alternate, the medial the largest, 6-10 cm. long, 1.3-2.0 cm. wide, 2-3 cm. distant, incised 0.8 their width, the lowermost reduced to less than 1 cm. long (often to 1 mm.), 5-6 cm. distant; segments spreading to slightly oblique (separated by a broad, rounded or acute sinus), 3-4 mm. broad, oblong, apex rounded or obtuse, the basal pair somewhat shortened (especially the anterior one); veins 7-9 pairs per segment; costae, veins, and leaf tissue below minutely puberulous with erect hairs 0.1 mm. long, also with scattered hamate hairs on leaf tissue (0.2 mm. long); leaf tissue above with numerous appressed hairs 0.1 mm. long; sori oblong, supramedial, exindusiate; $n = 29$.

Thelypteris balbisii (Spreng.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 10: 250. 1941. *Polypodium balbisii* Spreng. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 10: 228. 1821. *Aspidium sprengelii* Kaulf. Flora 6: 365. 1823. *Dryopteris sprengelii* (Kaulf.) O. Ktze. Rev. Gen. Pl. 2: 813. 1891. *D. balbisii* (Spreng.) Urban, Symb. Antill. 4: 14. 1903. *T. sprengelii* (Kaulf.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 65. 1953.

Along roadsides, trails, ditches, creek banks, near sea level to ca. 700 m.; Alta Verapaz; Baja Verapaz; Izabal. Southern Mexico; British Honduras; Nicaragua to Panama; Antilles; South America.

Rhizomes erect; stipes mucilaginous when young, mostly 3-6 mm. in diameter; fronds often 1 m. or more long, up to 40 cm. broad, with up to 10 pairs of gradually to subabruptly reduced pinnae at the base; rachises glabrous or with deciduous septate hairs up to 1.5 mm. long; largest pinnae (8) 10-16 (22) cm. long, 1.5-3.0 cm. broad, deeply incised to within 1 mm. of costae, usually opposite, horizontal; most pinnae with basal segments somewhat elongate; pinnae below with a peglike aerophore at the base; segments perpendicular or nearly so to the costae, linear, 2-3 mm. wide, rather closely placed; veins up to 18 pairs per segment; costae and costules sparsely hairy to often glabrous below, the hairs (if present) mostly simple, occasionally septate; leaf tissue below often with numerous orangish to reddish sessile hemispherical glands; sori medial to submarginal, with a persistent tan, often glandulose indusium.

Thelypteris caucaensis (Hieron.) Alston, J. Wash. Acad. Sci. 48: 233. 1958. *Nephrodium caucaense* Hieron. Bot. Jahrb. Syst. 34: 444. 1904. *Dryopteris caucaensis* (Hieron.) C. Chr. Index Fil. 257. 1905.

Rare, wet roadside banks and marshy meadows, 2,500-2,900 m.; San Marcos (*Steyermark 35978*, F; *Williams et al. 27010*, F, NY). Costa Rica; Colombia.

Rhizomes suberect; fronds 25-70 cm. long, with 2-3 pairs of lower pinnae reduced; stipes 8-35 cm. long, 1-3 mm. broad, tan or brownish; rachis hairy, hairs to 0.5 mm. long,

sometimes with a few scales; pinnae 3-6 cm. long, 1-1.5 cm. broad at the base, incised ca. 0.5-0.7 their width; segments 2-3 (4) mm. broad, obtuse to acutish at the tip; veins 5-7 pairs per segment; costae and costules below with scattered, stiff, antrorse, stout hairs mostly 0.3-0.5 mm. long, also with a few linear, sublathrate scales to 1 mm. long, these 2-3 cells wide; veins and leaf tissue on both sides glabrous, often shining; leaf tissue glabrous, dark green; sori supramedial to submarginal, exindusiate, with a few receptacular setae.

Guatemalan specimens are smaller than the type (Colombia), but agree in minute details. This species is evidently confined to high mountain peaks wherever it grows. In Guatemala, it is closely related only to *T. rudis*, but that species is much larger, with hairier, less coriaceous fronds. Sporangia of *T. caucaensis* are noticeably larger than those of *T. rudis*, suggesting that this species is polyploid.

Thelypteris cheilanthoides (Kunze) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 58. 1953. *Aspidium cheilanthoides* Kunze, Linnaea 22: 578. 1849. *Dryopteris cheilanthoides* (Kunze) C. Chr. Index Fil. 257. 1905. *D. lanipes* C. Chr. Smithson. Misc. Collect. 52: 394. 1909. *D. lanipes* C. Chr. forma *minor* C. Chr. loc. cit.

Uncommon, wet thickets, wooded ravines, 1,100-2,200 m.; Alta Verapaz; Guatemala? (types of *D. lanipes* and its f. *minor*, *Donnell-Smith* 2462, 2463, respectively, both US!); Quezaltenango; El Quiché; Sacatepéquez; Sololá; Suchitepéquez? Southern and western Mexico; Costa Rica; Jamaica; Hispaniola; Colombia and Venezuela to Peru, southern Brazil.

Rhizomes erect, caudex 2-4 (5) cm. thick; stipe bases to 1 cm. thick; fronds up to 2 m. long, usually mucilaginous when coiled, with 2-5 pairs of abruptly reduced basal pinnae, the lowermost glanduliform; rachis with stiff, whitish, multicellular hairs up to 2.5 mm. long, or glabrescent; pinnae 10-25 (30) cm. long, 1.5-3 (4) cm. broad, incised to within 1 (3) mm. of costae, with prominent aerophore at the base; segments usually falcate or subfalcate, with a revolute margin, ca. 3 mm. broad, basal segments often elongate, the basiscopic one the longest, often dentate and parallel to rachis; veins 12-18 (23) pairs per segment, usually immersed and blackened below; costae below usually with a few stiff multicellular hairs up to 2 mm. long; leaf tissue subsucculent when living, chartaceous to subcoriaceous when dried, glabrous on both sides, or with sessile yellowish to orange-red glands on leaf tissue below; sori submarginal (often partially hidden by revolute margin) with a relatively large, persistent indusium that is often glandular on the margin; $n = 29, 58$.

Tentatively, I place *Dryopteris lanipes* and forma *minor* in synonymy. Nearly all specimens of *T. cheilanthoides* have long (but fewer) septate hairs of the type described for *D. lanipes* by Christensen. The only other collection that approaches *D. lanipes* in density of septate hairs is *Steyermarck* 46796, F, from Volcán Santa Clara, Suchitepéquez.

Thelypteris cinerea (Sod.) A. R. Smith, *Phytologia* 34: 233. 1976. *Nephrodium cinereum* Sod. *Anales Univ. Centr. Ecuador* 22: 103. 1908. *Dryopteris sanctiformis* C. Chr. *Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII.* 10: 130, f. 12d. 1913. *T. sanctiformis* (C. Chr.) Reed, *Phytologia* 17: 312. 1968.

Uncommon, wet shaded banks and sand cliffs, ca. 2,000-2,500 m.; Quezaltenango; San Marcos. Southern Mexico; Costa Rica; Panama; Venezuela; Ecuador.

Rhizomes erect; stipes fasciculate, 6-12 cm. long, ca. 1-1.5 mm. in diameter, brownish, shining, glabrous; rachises minutely puberulous by hairs less than 0.1 mm. long; laminae narrowly lanceolate, deeply bipinnatifid, up to 25 cm. long, 3-7 cm. broad, lowermost 1-3 pairs reduced and auriculiform; pinnae ca. 15 pairs, inequilateral with the basiscopic side narrower, 2-4 cm. long, up to 1.3 cm. broad, falcate; segments oblique, 2-3 mm. broad, obtuse to acute at the apex; veins 3-5 pairs per segment; costae above setose, below glabrous or minutely puberulous; leaf tissue on both sides glabrous or with sessile yellowish glands below; sori medial, with large persistent indusia up to 1 mm. in diameter, these glossy, reddish brown, often sessile-glandular; $n = 29$.

Thelypteris concinna (Willd.) Ching, *Bull. Fan Mem. Inst. Biol. Bot.* 10: 251. 1941. *Polypodium concinnum* Willd. *Sp. Pl.* 5: 201. 1810. *Dryopteris concinna* (Willd.) O. Ktze. *Rev. Gen. Pl.* 2: 812. 1891.

Wet forests, wooded ravines, along streams, 1,500-1,950 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Huehuetenango; Sacatepéquez. Eastern and southern Mexico; El Salvador and Honduras to Venezuela and northwestern Argentina; West Indies.

Rhizomes suberect; stipes up to ca. 15 (25) cm. long, 2-5 mm. in diameter, brownish; aerophores absent; laminae with up to 12 pairs of gradually reduced basal pinnae, up to ca. 80 cm. long, 15 (20) cm. broad; pinnae up to ca. 30 pairs, 8-14 cm. long, 1-2 cm. broad, incised to ca. 1 mm. from costae; segments slightly oblique, obtuse to subacute at the apex, ca. 2 mm. broad; veins mostly 6-8 (10) pairs, meeting the margin above the sinus; costae and rachises below minutely but densely and evenly puberulous, hairs less than 0.1 mm. long, not hamate; leaf tissue chartaceous, below glabrous, eglandulose, above with appressed hairs 0.1 mm. long, glabrescent; sori supramedial, exindusiate; sporangia minutely setose; $n = 29$.

Thelypteris deflexa (Presl) Tryon, *Rhodora* 69: 5. 1967. *Nephrodium deflexum* Presl, *Rel. Haenk.* 1: 36, t. 5, f. 2. 1825. *Dryopteris lindigii* C. Chr. *Index Fil.* 275. 1905. *T. lindigii* (C. Chr.) Alston, *J. Wash. Acad. Sci.* 48: 233. 1958.

Rare, forested slopes of ravine along stream, 2,400 m.; Huehuetenango (sole Guatemalan collection seen: *Steyermark 50013*, F.). Southern Mexico; Honduras; Costa Rica; Colombia and Venezuela to Peru.

Rhizomes erect or suberect, caudex ca. 1-1.5 cm. thick; fronds mostly 30-60 cm. long, with 2-4 pairs of reduced basal pinnae; stipes stramineous with a blackened base, sparsely scaly at the base (scales tan, ovate, ca. 3 mm. long, glabrous), otherwise glabrous, 5-12 cm. long, 1-2 mm. broad; rachises glabrous below; pinnae horizontal or somewhat deflexed, opposite or subopposite, mostly 3-6 (9) cm. long, 0.7-1.2 (1.7) cm. broad (broadest at the base), incised to within 1 (1.5) mm. of costae; segments slightly oblique, rounded at apex, ca. 2-3.5 mm. broad; veins 4-6 pairs per segment; costae, veins, and leaf tissue below glabrous, or sparsely hairy on costae, glabrous above except along costae; leaf tissue thin, herbaceous; sori medial, exindusiate; $n = 58$.

Thelypteris linkiana (Presl) Tryon, *Rhodora* 69: 6. 1967. *Grammitis linkiana* Presl, Tent. Pterid. 209. 1836. *Gymnogramma diplazioides* Desv. Mém. Soc. Linn. Paris 6: 214. 1827, as *G. diplazioides*. *Dryopteris diplazioides* (Desv.) Urban, Symb. Antill. 4: 21. 1903. *D. linkiana* (Presl) Maxon, J. Wash. Acad. Sci. 14: 199. 1924. *T. diplazioides* (Desv.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 59. 1953, not *T. diplazioides* (Moritz ex Mett.) Ching, 1936.

Uncommon, wet forests and gullies, 1,400-1,600 m.; Alta Verapaz; Baja Verapaz; Suchitepéquez? Southern Mexico; Costa Rica; Antilles; Colombia to Bolivia, southern Brazil.

Rhizomes erect; fronds 60-140 cm. long, with 2-6 lowermost pinnae reduced, the lowermost 2 cm. long or more, often short-stalked (ca. 1 mm.); stipes 15-25 cm. long; proliferous buds nearly always present in axils of upper pinnae; pinnae 8-13 cm. long, 1.5-2.5 cm. broad (broadest at the base), incised 0.5-0.7 their width, with a small tuberculiform aerophore at the base of larger pinnae; segments oblong, 4-6 mm. broad, rounded to truncate at apex, spreading or slightly oblique; veins 4-8 pairs, the lowermost meeting the margin at or slightly above the sinus; costae and veins below with scattered hamate hairs ca. 0.2 mm. long; leaf tissue on both sides glabrous or glabrescent, or with appressed hairs 0.1 mm. long above; sori oblong to linear (to ca. 2 mm.), exindusiate; $n = 29, 58$.

Thelypteris melanochlaena (C. Chr.) Reed, *Phytologia* 17: 292. 1968. *Dryopteris melanochlaena* C. Chr. *Smithson. Misc. Collect.* 52: 384. 1909.

Moist slopes, forested ravines, 1,100-2,000 m.; Alta Verapaz (type near Cobán, *Donnell-Smith 168*, part, US); Baja Verapaz; Chiquimula; Quezaltenango. Southern Mexico; Honduras.

Rhizomes suberect; stipes 5-10 cm. long, 2.5-3.5 mm. in diameter, deciduously pubescent; laminae up to 60 cm. long, 8-22 cm. broad, at the base with 7-14 pairs of gradually reduced pinnae; pinnae 4-12 cm. long, 1.2-2.2 cm. broad, up to 30 pairs, deeply pinnatifid to within 1 mm. of costae; segments patent or slightly oblique, ca. 2.5-3.5 mm. broad, rounded or subacute at the apex; veins 7-10 pairs; costae on both sides with patent (below) or adpressed (above) hairs 0.2-0.3 mm. long, without scales; leaf tissue below with numerous patent hamate hairs ca. 0.2 mm. long, above appressed-puberulent with hairs ca. 0.1 mm. long; sori supramedial to submarginal, with a dark-brown to blackish shining indusium, indusia ciliate-margined; sporangia glabrous; $n = 58$.

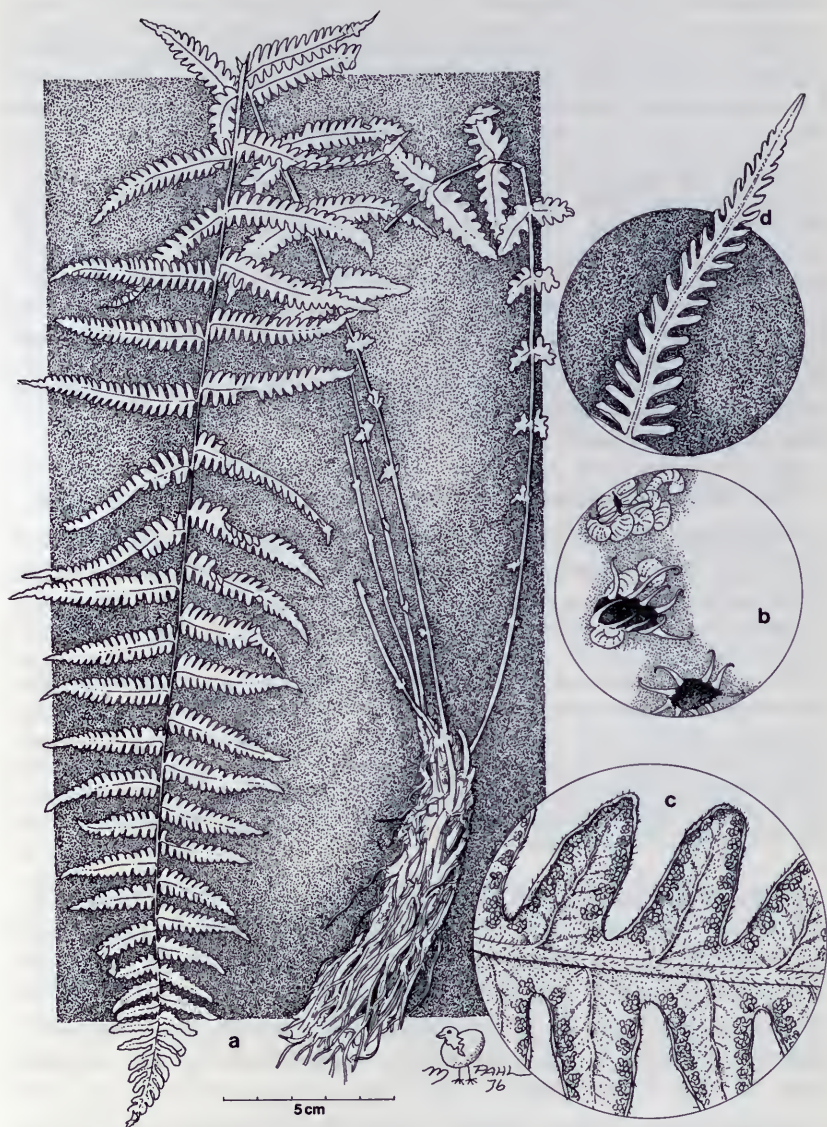


FIG. 75. *Thelypteris* subgenus *Amauropelta*. *T. melanochlaena*. a, habit, $\times \frac{1}{2}$; b, sori, showing blackish indusia and hamate hairs, greatly enlarged; c, portion of fertile pinna, $\times 5$; d, pinna, $\times 1$.

Thelypteris nubigena A. R. Smith, Proc. Calif. Acad. Sci. Ser. 4. 40: 229. f. 7, C. 1975. *Lagarta*.

Higher elevation cloud forests (Mexico), 2,500-3,700 m.; Quezaltenango. Known from single collections from Oaxaca, Chiapas (type from Zontehuiz, *Breedlove 22057* [with *Smith*], DS), and Guatemala (Volcán Santo Tomás, *Steyermark 34709*, F').

Rhizomes suberect; stipes to 15 cm. long, 3 mm. broad, darkened and sparsely scaly at the base, the scales ovate, tan, sparsely hairy on the margin, less than 2 mm. long; fronds to ca. 65 cm. long, with 4-5 lowermost pairs of pinnae gradually reduced, the lowest to ca. 1 mm.; pinnae ca. 25 pairs, the largest 7-11 cm. long, 1.8-2.3 cm. wide, widest at the base, lobed ca. 0.9 toward the costae; segments oblique, subfalcate, up to 10 mm. long, 2 mm. broad, rounded to subacute at the apex; veins up to 10 pairs per segment; aerophores up to 1 mm. long at base of lower pinnae; rachises, costae, and costules on both sides epaleate, with scattered straight hairs ca. 0.2 mm. long, the hairs often in pairs or threes (subfasciculate); glands on lower surfaces numerous, orangish to reddish, sessile, hemispherical; sori medial; indusia minute, fringed or completely obscured by orangish glands.

Thelypteris oaxacana A. R. Smith, Amer. Fern J. 63: 125. 1973.

Not known from Guatemala, but to be expected at middle elevations (1,650-2,150 m.) in montane rain forest. Southern Mexico; El Salvador.

Rhizomes erect; fronds ca. 60-95 cm. long, 14-25 cm. broad, with 6-10 pairs of gradually reduced basal pinnae, young fronds mucilaginous; stipes up to 15 cm. long, 5 mm. in diameter; rachis above with scattered hairs along the sulcus, glabrous below; pinnae 1.3-2.1 cm. wide, broadest at their base, incised ca. 0.8 times their width, with prominent aerophores at their base; segments 3-5 mm. wide; slightly oblique, not falcate, with rounded or subacute apex; veins 5-8 pairs per segment, glabrous; costae above with scattered acicular hairs 0.5 mm. long, below epilose and toward the base with a few linear-lanceolate stramineous appressed scales; leaf tissue glabrous on both sides; sori medial, round or slightly oblong, with a prominent, persistent, glabrous indusium ca. 0.7 mm. in diameter; sporangia glabrous.

Thelypteris oligocarpa (Humb. & Bonpl. ex Willd.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 10: 253. 1941. *Polypodium oligocarpum* Humb. & Bonpl. ex Willd. Sp. Pl. ed. 4. 5: 201. 1810. *Dryopteris oligocarpa* (Humb. & Bonpl. ex Willd.) O. Ktze. Rev. Gen. Pl. 3: 378. 1898. *D. columbiana* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 4: 279, f. 8. 1907. *T. columbiana* (C. Chr.) Morton, Leaf. W. Bot. 8: 194. 1957.

Common along stream banks, wet thickets, forested slopes, 600-1,800 m.; Alta Verapaz; Baja Verapaz; Chiquimula; Guatemala; Huehuetenango; Santa Rosa. Mexico (Nayarit and Tamaulipas to Chiapas); Honduras; Costa Rica; Panama; Greater Antilles; Colombia to Venezuela and Bolivia.

Rhizomes erect; fronds mostly (30) 40-75 cm. long with 3-6 pairs of reduced basal pinnae, the lowest of these a few mm. long, 5-6 cm. apart; stipes 4-13 cm. long, 2-3 mm. in diameter, often brownish, puberulous; rachises below usually with dense short hairs ca. 0.2 mm. long, or with a few longer hairs intermixed; pinnae ca. 20 pairs, the largest 5-8 (10) cm. long (1.0) 1.2-2.0 (2.6) cm. broad, deeply incised to within 1 mm. of costae; segments oblique, subfalcate, 2-3 mm. broad, obtuse to acutish; veins 8-10 pairs per segment; costae, veins, and leaf tissue below with numerous hairs mostly 0.2-0.4 mm. long, also with a few hamate hairs on leaf tissue, above with stout, stiff hairs 0.5-1.0 mm. long on costae, costules, and veins, both sides eglandulose; leaf tissue thin; sori supra-medial to submarginal, with a very small indusium (concealed by mature sporangia) that is short-ciliate on the margin; $n = 29$.

Most Guatemalan and Mexican specimens of this species match perfectly the type of *D. columbiana* (from Colombia), which Christensen distinguished from *D. oligocarpa* by the latter's having longer hairs on the rachis, pinnae more closely placed, and smaller blades. None of these distinctions seems to be taxonomically usable when a large series of specimens from throughout tropical America is studied; hence I apply the oldest name to Guatemalan specimens. Monographic revision is needed.

***Thelypteris pilosa-hispida* (Hook.) Alston, J. Wash. Acad. Sci. 48: 233. 1958. *Nephrodium piloso-hispidum* Hook. Sp. Fil. 4: 105. 1862. *Dryopteris piloso-hispida* (Hook.) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 148. 1913.**

Wet mixed forests, shaded banks, ca. 1,500 m.; Alta Verapaz; Baja Verapaz. Southern Mexico; Honduras to Ecuador; Hispaniola.

With the characters of *Thelypteris rudis*, but differing from that in having segments more or less perpendicular to the costae, not falcate, the margin only slightly or not at all revolute; costae below with hairs longer (up to ca. 1 mm. long), softer, spreading rather than antrorse; costal scales larger, castaneous, not so clathrate; receptacle with a few stiff acicular hairs; $n = 29$.

This uncommon species is known from Guatemala by about six collections from Alta Verapaz and one from Baja Verapaz; the species seems to grow at generally lower elevations than its nearest relative, *T. rudis*, both in Guatemala and in southern Mexico.

***Thelypteris pilosula* (Mett.) Tryon, Rhodora 69: 7. 1967. *Aspidium pilosulum* Mett. Fil. Hort. Bot. Lips. 130. 1856. *Dryopteris pilosula* (Mett.) Hieron. Hedwigia 46: 332. 1907.**

Stream banks, mixed wet forests, shaded ravines, 1,800-3,300 m.; Baja Verapaz; Chimaltenango; Guatemala; Huehuetenango; Quezaltenango; Sacatepéquez; San Marcos; Totonicapán. Mexico (Jalisco and Hidalgo to Chiapas); Honduras and El Salvador to Peru; Jamaica; Hispaniola.

Rhizomes erect; fronds 50-100 cm. long, up to 35 cm. broad, with ca. 5-7 pairs of gradually reduced basal pinnae, croziers not mucilaginous; stipes (and rachises) tan to brownish, up to 25 cm. long, 5 mm. in diameter, strigose with hairs mostly 1 mm. long or more, with persistent spreading linear-lanceolate scales at the base; pinnae 1.5-2.2 cm. wide, incised ca. 0.8-0.9 times their width, without aerophores; segments 3-4 mm. broad, oblique, not (or slightly) falcate, apex rounded to subacute; veins 6-10 pairs per segment; costae, costules, and veins above and below with stout patent, acicular hairs mostly 0.5-1.0 mm. long, epaleate; leaf tissue glabrous on both sides, chartaceous (infrequently subcoriaceous); sori medial to supramedial, with prominent, persistent, marginally setose indusia ca. 0.4 mm. in diameter, indusia also with a few minute short-stipitate glands; sporangia glabrous; $n = 29$, 58.

Proctor 25305 (US), from a wet springy meadow north of Nebaj, Dept. El Quiché, is most similar to *T. pilosula* but differs in having a creeping rhizome, much smaller indusia, shorter and less stout hairs on the veins above, and less numerous, ovate, more or less appressed stipe base scales. It probably represents an undescribed species, but I hesitate to describe it on the basis of this single collection.

Thelypteris resinifera (Desv.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 63. 1953. *Polypodium resiniferum* Desv. Berlin Mag. 5: 317. 1811. *Nephrodium panamense* Presl, Rel. Haenk. 1: 35. 1825. *Dryopteris panamensis* (Presl) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 4: 292. 1907. *D. resinifera* (Desv.) Weatherby, Contr. Gray Herb. 114: 32. 1936. *T. panamensis* (Presl) E. St. John, Amer. Fern J. 26: 44. 1936.

Common along shaded banks, streams, and roadside ditches, in damp ravines and thickets, 50-2,300 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Escuintla; Guatemala; Izabal; Jalapa; Quezaltenango; Retalhuleu; Santa Rosa; San Marcos; Zacapa. Florida; southern and western Mexico; British Honduras; El Salvador and Honduras to Panama; Greater Antilles.

Rhizomes erect; stipes stramineous to tan, usually mucilaginous when young, 1-3 (6) mm. in diameter; fronds (15) 25-100 (130) cm. long with up to 12 pairs of gradually reduced pinnae at the base, the stipes mostly less than 5 (15) cm. long; rachises hairy to glabrescent, the hairs simple, up to ca. 0.5 mm. long; largest pinnae to 13 cm. long, (0.4) 0.7-1.5 cm. broad, incised to within 1 mm. of costae; pinnae below with tuberculiform aerophores at their base, ascending in the upper two-thirds of the lamina; segments very oblique to the costae, often falcate, deltoid to lanceolate, up to ca. 2.5 mm. broad; veins (3) 5-10 pairs per segment; costae and costules usually short-hairy below, the hairs simple, mostly less than 0.3 mm. long; leaf tissue below usually with numerous golden to reddish, sessile, hemispherical, resinous glands, these uncommonly absent; sori medial, with a persistent tan, usually glandulose indusium; sporangia glabrous; $n = 29$, 58?

Closely related to *T. opposita* (Vahl) Ching, from which it differs in having longer, more oblique and falcate segments; *Thelypteris opposita* is a common species in the Lesser Antilles and South America.

In Mexico and Central America, *T. resinifera* comes closest to *T. struthiopteroides*, and a few specimens seem to be intermediate between the two species. Ordinarily, *T. resinifera* is a smaller species with more falcate segments; presence or absence of pubescence and glands is, however, the most reliable means of separating the two.

Thelypteris rudis (Kunze) Proctor, Bull. Inst. Jamaica. Sci. Ser. 5: 64. 1953. *Polypodium rude* Kunze, Linnaea 13: 133. 1839. *Dryopteris rudis* (Kunze) C. Chr. Index Fil. 289. 1905.

Wet mixed forests, wooded ravines, and stream banks, 1,375-2,800 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; El Progreso; Huehuetenango; Quezaltenango; Sacatepéquez; San Marcos; Sololá; Totonicapán. Southern and western Mexico (type from Veracruz, Jalapa, *Schiede s.n.*); El Salvador and Honduras to Venezuela and Bolivia; Greater Antilles.

Rhizomes suberect; stipes up to ca. 25 (45) cm. long, 2-5 (8) mm. in diameter, darkened, often bearing tuberculiform aerophores at intervals of 2-3 (7) cm., pubescent (infrequently glabrescent); laminae (including "abortive" pinnae) (35) 50-100 (125) cm. long, up to 45 cm. broad, toward the base with (3) 5-12 pairs of wartlike pinnae that can be easily overlooked; developed pinnae (5) 10-22 cm. long, (1) 1.5-3 (4.5) cm. broad, with a small aerophore at the base; segments slightly oblique and subfalcate, ca. 3-5 mm. broad, rounded to acutish at the apex, the margin slightly revolute; basal pair of segments considerably reduced in the lower pinnae; costae below antrorsely strigose and with brownish to blackish subclathrate scales especially toward the base; leaf tissue dark green when dried, chartaceous to subcoriaceous, pubescent on both sides or glabrous, the hairs mostly 0.2-0.3 mm. long, those below sometimes hamate; sori supramedial, exindusiate; sporangia glabrous; $n = 29$.

This species and *T. pilosula* are by far the most common species of subg. *Amauropelta* in Guatemala. Both occupy similar habitats at middle to higher elevations. *Thelypteris rudis* is easily distinguished from *T. pilosula* by the presence of clathrate scales on costae below and by the absence of indusia. Specimens of *T. rudis* vary greatly in size but all share the diagnostic set of microscopic characters.

Thelypteris sancta (L.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 10: 254. 1941. *Acrostichum sanctum* L. Syst. Nat. ed. 10. 2: 1320. 1759. *Dryopteris sancta* (L.) O. Ktze. Rev. Gen. Pl. 2: 813. 1891.

Uncommon, wooded slopes, 250-300 m.; Alta Verapaz; Petén; Sacatepéquez. Antilles.

Rhizomes erect, up to 1.5 cm. thick; fronds numerous, tufted, mostly 15-40 cm. long; stipes mostly 3-5 cm. long, ca. 1 mm. in diameter, stramineous; laminae up to ca. 35 cm. long, oblanceolate, attenuate at the apex, the lower pinnae (several pairs) evenly reduced, auriculate or unequally 3-foliate; largest pinnae up to 5 cm. long, 4-12 mm. broad, usually inequilateral at the base, very deeply pinnatifid; segments strongly oblique, 1-2

mm. broad, rounded at the apex, entire or crenate-serrate, the basal pair often free, veins 2-6 (10) pairs per segment; costae, costules, veins, and leaf tissue below glabrous or finely hirtellous, sometimes resinous-glandular; leaf tissue thin, herbaceous to chartaceous; indusium very small, ciliate, sometimes resinous-glandular; $n = 29$.

The four Guatemalan collections that I have seen (*Steyermark 44699*, F; *Salvin & Godman 31*, K; *Tuerckheim s.n.*—ed. Donn.-Sm. 8353, GH, NY; *Contreras 2405*, MICH) are apparently the only certain records from continental America. They differ from most Antillean specimens in being eglandular, but are otherwise very similar.

Thelypteris scalaris (Christ) Alston, J. Wash. Acad. Sci. 48: 234. 1958. *Aspidium scalare* Christ, Bull. Herb. Boissier II. 6: 159. 1906. *Dryopteris scalaris* (Christ) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 4:323. 1907.

Uncommon, wet shaded banks, 350-550 m.; Alta Verapaz (lectotype from Cubilguitz, *Tuerckheim s.n.* [P], chosen by Christensen, *tom. cit.* 324). Southern Mexico; Costa Rica; Panama; Colombia?

Rhizomes suberect to erect; fronds to 1.1 m. long, with 7-11 pairs of gradually reduced basal pinnae, lowermost auriculiform, ca. 5 mm. long; stipes to ca. 8 cm. long, 2-3 mm. broad with densely short-hairy scales at the base; buds sometimes present toward distal part of rachis; pinnae subopposite, horizontal, to 45 pairs, the largest 6-11 cm. long, 1.1-2.6 cm. broad, incised to ca. 1 mm. from costae; segments 2-4 mm. broad, mostly rounded at the tip, perpendicular to costae; veins 9-12 pairs per segment; costae and veins below with scattered to dense hairs to 0.3 mm. long; leaf tissue herbaceous, below with erect hamate hairs to 0.3 mm. long, above rather densely appressed-hairy (hairs 0.1 mm.); sori supramedial, with a small indusium that is marginally hamate-hairy; $n = 29$.

Thelypteris struthiopteroides (C. Chr.) Reed, Phytologia 17: 316. 1968. *Dryopteris struthiopteroides* C. Chr. Smithson. Misc. Collect. 52: 388. 1909.

Damp thickets and banks, 240-1,300 m.; Escuintla (type from Concepcion, *Donnell-Smith 2459*, US! fragment BM!); Quezaltenango; Retalhuleu; San Marcos; Suchitepéquez. Chiapas.

With the characters of *Thelypteris balbisii*, but differing from that in having rather oblique segments and in the complete lack of acicular or long-septate hairs on the rachises, costae, or leaf tissue below; sparsely glandular to seemingly glabrous on indusial margins and leaf tissue below; lower pinnae usually gradually (not subabruptly) reduced.

In many respects this species is intermediate between *T. resinifera* and *T. balbisii*, its two closest relatives. From the former it differs in the constantly glabrous fronds and broader, more deeply incised pinnae. Enough collections have now been made in western Guatemala and southwestern Chiapas to show that *T. struthiopteroides* has a nicely circumscribed, although apparently limited, range.

Thelypteris thomsonii (Jenm.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 65. 1953. *Polypodium thomsonii* Jenm. J. Bot. 24: 272. 1886. *Dryopteris stuebelii* Hieron. Hedwigia 46: 340. 1907. *D. thomsonii* (Jenm.) C. Chr. Index Fil. 298. 1905.

Wet forested ravines, 2,500-2,700 m., San Marcos (*Standley 86349*, F). Southern Mexico; El Salvador; Costa Rica; Colombia; Ecuador (type); Jamaica; Hispaniola.

Rhizomes erect, massive; stipes stramineous to tan, mucilaginous when young, 6-10 mm. wide, with numerous partly appressed tan scales up to ca. 8 mm. long, 5 mm. broad; fronds large, up to 1.5 m. (or more?) long, with pinnae abruptly reduced toward the base and numerous wartlike pinnae less than 5 mm. long; largest pinnae up to 32 cm. long, 2.0-4.4 cm. broad, deeply incised to within 1 mm. of costae, lower pinnae somewhat narrowed at the base; prominent squamate aerophores up to 6 mm. long at base of costae below, with smaller aerophores up to 1 mm. long often present at base of costules; veins up to 25 pairs per segment; costae and costules below densely hairy with fasciculate hairs ca. 0.1 mm. long; leaf tissue below with numerous reddish sessile hemispherical glutinous glands; indusia small, nearly obscured by dense reddish glands like those of the lamina; sporangia glabrous; $n = 58$.

THELYPTERIS subg. **CYCLOSORUS** (Link) Morton, Amer. Fern J. 53: 153. 1963. *Cyclosorus* Link, Hort. Reg. Bot. Berol. 2: 128. 1833. *Dryopteris* subg. *Cyclosorus* (Link) C. Chr. Index Fil. XXI. 1906.

Rhizomes creeping to erect; laminae pinnate-pinnatifid, the lowermost pinnae reduced or not (most American spp.); aerophores absent or only a small darkened protuberance; lowermost veins of segments meeting the margin at the sinus or connivent just below the sinus or meeting below the sinus with an excurrent vein to the sinus; costae and veins below with unbranched, unicellular, acicular hairs and sometimes capitate glands; sori round, with a usually large, persistent, hairy indusium; sporangia with or without hairs or glands from sporangial stalks; spores bilateral, dark, with an often broadly winged perispore; $x = 36$.

In his revision of genera of Thelypteridaceae in the Old World, Holttum (*Blumea* 19: 17-52. 1971) restricted the application of *Cyclosorus* to the type species, *Aspidium gongylodes* (= *Thelypteris interrupta* s.l.) and one other African species. Later (*J. South African Bot.* 40: 123-168. 1974), he concluded that the American species previously ascribed to *Cyclosorus* by Christensen and others had closest affinities to *Christella*, with perhaps 50 Old World species. While *Thelypteris dentata* and *T. hispidula* in the New World certainly do have affinities in *Christella*, I believe that the affinities of the remaining American *Cyclosorus* are still obscure; hence I apply the name in a broader sense than does Holttum. Subgenus *Cyclosorus* in the New World contains 18 species, from southeastern United States, southern California, Arizona, and Mexico to northern Argentina and the Antilles. The greatest number of species is in southern Mexico and Guatemala.

- a. Basal veins of adjacent segments united below the sinus with an excurrent vein to the sinus; costules, veins, and often leaf tissue above hairy.
- b. Rhizomes long-creeping (often with more than 3 cm. between stipe bases), black, nearly naked; costae below with tan scales; leaf tissue above usually glabrous. *T. interrupta*.
- b. Rhizomes short-creeping to erect, brown, with inconspicuous scales; costae below without scales; leaf tissue and veins above pubescent with stout hairs.
- c. Costae below with predominantly short, uniform hairs less than 0.1 (0.2) mm. long; stipes and rachises usually darkened; rhizomes short-creeping. *T. dentata*.
- c. Costae below with most hairs greater than 0.3 mm. long with many exceeding 0.5 mm.; stipes and rachises usually stramineous; rhizomes suberect. *T. hispida*.
- a. Basal veins of adjacent segments free or connivent at the sinus; costules, veins, and leaf tissue above with or without hairs.
- d. Rachis and upper part of stipe conspicuously scaly. *T. tuerckheimii*.
- d. Rachis and upper part of stipe not conspicuously scaly.
- e. Rhizomes erect, the caudex 2-5 cm. in diameter, the stipes straight at base; basal segments of lower and medial pinnae usually elongate parallel to rachis; prominent auricles often present at base of lower pinnae; costae below without scales. *T. patens*.
- e. Rhizomes long- to short-creeping, the stipes arcuate at the base; basal segments of lower and medial pinnae not greatly enlarged to form auricles, in some species reduced; costae below with or without scales.
- f. Costae and often costules and veins above with at least a few rather stout hairs, mostly greater than 0.3 mm. long; lamina above often capitate-glandular. *T. kunthii*.
- f. Costae, costules, and veins above glabrous or with very thin, short hairs mostly less than 0.2 mm. long, predominantly along the costae; leaf tissue above eglandular.
- g. Terminal "pinna" at least 5 times as long as wide; scales on costae below often numerous, mostly greater than 0.8 mm. long; texture coriaceous; lower pinnae often less than 1.2 cm. wide, more than 12 times longer than wide. *T. augescens*.
- g. Terminal "pinna" less than 5 times as long as wide; scales absent or occasional on costae below, these often less than 0.8 mm. long; texture chartaceous to coriaceous; lower pinnae usually greater than 1.2 cm. broad, less than 12 times longer than wide.
- h. Stipe base scales very dark brown, bristle-like; indusia densely long-hairy; costae below glabrous or sparsely hairy. *T. blepharis*.
- h. Stipe base scales tan, linear-lanceolate to ovate-lanceolate; indusia hairy or glabrous; costae below hairy or glabrous.
- i. Scales few, narrow, 1-3 mm. long, persistent on the rachis; basal segments of pinnae usually somewhat elongate parallel to rachis; pinnae incised more than 0.8 their width; sori submarginal; hairs on costae below and indusia below sparse or moderately dense, acicular. *T. ovata* var. *lindheimeri*.
- i. Scales mostly absent from rachis, if present less than 1 mm. long; basal segments of pinnae not elongate parallel to rachis; pinnae incised 0.7-0.8

their width; sori medial to submarginal; indusia and costae below glabrous or with dense subflexuous hairs.

j. Indusia, costae, and leaf tissue below with short, rather dense hairs.

T. puberula var. *puberula*.

j. Indusia and costae below glabrous or sparsely hairy. . *T. cretacea*.

Thelypteris augescens (Link) Munz & Johnston, Amer. Fern J. 12: 75. 1922. *Aspidium augescens* Link, Fil. Sp. 103. 1841. *Dryopteris augescens* (Link) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 182. 1913.

Sun or partial shade on limestone banks, low elevations; Petén (a single collection, *Contreras 3624*, US). Southern Florida; Bahamas; Cuba.

Rhizomes creeping, 0.4-0.8 cm. in diameter; fronds (30) 65-140 cm. long with a \pm distinct terminal pinna (5) 7-17 cm. \times 1-3 (5) cm.; stipes about as long as lamina, 2-7 (9) mm. in diameter, paleate at the base, the scales linear-lanceolate, castaneous, shining, ciliate on the margin; largest pinnae (4) 10-22 (28) cm. long, (0.3) 0.7-1.5 cm. wide, incised 0.5-0.7 their width; lower pinnae with basal segments slightly longer and narrower than more distal segments; basiscopic segment of distal pinnae adnate to rachis; segments subfalcate, the margin revolute; veins (3) 5-8 (10) pairs per segment, the basal pair connivent at the sinus; scales on costae below mostly 0.6-1.0 mm. long, castaneous and ciliate; costae, costules, and leaf tissue below pubescent (hairs 0.2-0.4 mm. long), above glabrous except along costae, eglandular; leaf tissue coriaceous; indusia with hairs mostly 0.2-0.4 mm. long; paraphyses lacking; spores (39) 44-55 (60) μ m. long; $n = 72$.

Thelypteris blepharis A. R. Smith, Proc. Calif. Acad. Sci. Ser. 4. 40: 227, f. 7, *F-H*. 1975.

Forested ravines, on limestone, 2,300-2,400 m.; Huehuetenango (a single collection, *Steyermark 49997*, F). Mexico (Chiapas, type from munic. La Independencia, road from Las Margaritas to Campo Alegre, *Breedlove 33605*, DS).

Rhizomes creeping; stipes 20-40 cm. long, 4-6 mm. in diameter, brownish or weakly purplish, bearing numerous spreading linear-lanceolate scales up to 8 mm. long, 1 mm. wide, these glabrous or minutely glandular on the margin, dark-castaneous, shining; rachises with a few similar scales, tan; blades chartaceous or subcoriaceous, dark green, 50-70 cm. long, 30-36 cm. broad, gradually tapering to a pinnatifid apex; pinnae up to 19 cm. long, 2.1 cm. broad, incised nearly to the costae; segments oblique, subfalcate, acute or obtuse at the apex, the basal segments of the lower pinnae only slightly or not at all enlarged; veins up to 13 pairs per segment, the lowermost meeting the margin at or just above the sinus; rachises, costae, and veins below without hairs or sparsely hairy, sometimes with scattered stipitate yellowish minute glands, above with hairs up to ca. 0.5 mm. long along the costae and rachises; leaf tissue on both sides glabrous; sori medial; indusia reddish brown, glandular, densely long-hairy, with hairs up to ca. 1 mm. long.

Thelypteris cretacea A. R. Smith, Univ. Calif. Publ. Bot. 59: 92, f. 118, C. 1971.

Uncommon, rocky outcrops along streams, wooded slopes, 200-400 m.; Chiquimula; Santa Rosa. Southern Mexico; El Salvador; Nicaragua; Costa Rica (type).

Rhizomes short-creeping, paleate at the apex, the scales tan, ovate-lanceolate, 3-4 mm. \times 1-1.5 mm., glabrous, with cells \pm isodiametric; fronds 20-60 (100) cm. long; stipes 5-35 (50) cm. long, 1.5-4 (7) mm. wide, stramineous, basal scales like those of rhizome, otherwise glabrous; rachises glabrous or with short-stalked glands; laminae gradually tapering distally; pinnae 5-10 (17) cm. long, (0.6) 0.9-1.5 (2.1) cm. wide, incised (0.5) 0.7-0.8 their width, widest at the base; segments oblique, subfalcate, 2-3 (4) mm. wide, basal segments of lower pinnae sometimes slightly auriculate; veins (4) 6-9 (12) pairs per segment, lowermost meeting margin at the sinus or nearly so; costae, veins, and leaf tissue glabrous on both sides or below with sparse hairs 0.3 mm. long and/or glands, these stalked (less than 0.1 mm. long), yellowish, often numerous; sori supramedial, with glabrous or very sparsely hairy indusia, also with numerous glands; spores 34-43 μ m. long; $n = 36$.

I now regard *Standley 89843* (F, US), cited by me (1971) as this species, to be instead an unusually glabrous specimen of *T. patens*. The specimen at F shows that the rhizome is erect. This species seems to occur most commonly on the Pacific slope, often along rocky stream banks in drier areas.

Thelypteris dentata (Forssk.) E. St. John, Amer. Fern J. 26: 44. 1936. *Polypodium dentatum* Forssk. Fl. Aegypt.-arab. 185. 1775. *Aspidium molle* Swartz, J. Bot. (Schrader) 1800 (2): 34. 1801. *Dryopteris mollis* (Swartz) Hieron. Hedwigia 46: 348. 1907. *D. dentata* (Forssk.) C. Chr. Kongel. Danske Vidensk. Selsk. Skr. Naturv. Afd. VIII. 6:24. 1920. *Cyclosorus dentatus* (Forssk.) Ching, Bull. Fan Mem. Inst. Biol. Bot. 8: 206. 1938.

Naturalized in the New World, wet meadows, ditches, edges of woods, 0-1,500 m.; Baja Verapaz; Chimaltenango; Guatemala; Izabal; Sololá, probably elsewhere. Southeastern United States; southern Mexico, Nicaragua; Costa Rica; South America; West Indies; Old World tropics and subtropics.

Rhizomes short-creeping; fronds somewhat dimorphic, the sterile shorter and with fewer, wider pinnae than the fertile; stipes darkened, often purplish, 15-45 cm. long, 3-5 mm. in diameter, paleate at the base; blades herbaceous or chartaceous, (24) 40-92 cm. long, tapering evenly toward the pinnatifid apex; largest pinnae 7-17 cm. long, 1.1-2.7 cm. wide, incised 0.5-0.8 of the way to the costae; lower (1) 2-6 pairs of pinnae reduced, auricled at the superior base, the auricles entire or crenate; veins 6-10 pairs per segment, the basal pair from adjacent segments united at an obtuse angle below the sinus with an excurrent veinlet 2-4 mm. long; costae, costules, and leaf tissue pubescent below, the hairs dense, uniformly short, 0.1-0.2 mm. long, occasionally with scattered

longer hairs, above with hairs longer and stouter except on leaf tissue; glands usually absent on blades; indusia uniformly pubescent, with hairs 0.1-0.2 mm. long; $n = 72$.

Thelypteris hispidula (Decne.) Reed, *Phytologia* 17: 283. 1968. *Aspidium hispidulum* Decne. *Nouv. Ann. Mus. Hist. Nat.* 3: 346. 1834. *Nephrodium quadrangulare* Fée, *Gen. Fil.* 308. 1852. *Dryopteris quadrangularis* (Fée) Alston in Box & Alston, *J. Bot.* 75: 253. 1937. *T. quadrangularis* (Fée) Schelpe, *J. South African Bot.* 30: 196. 1964.

Damp thickets, forests, stream banks, 0-1,000 m.; Alta Verapaz; Escuintla; Izabal. Southeastern United States; western and southern Mexico; British Honduras; Honduras and El Salvador to Panama; Antilles; South America (to northern Argentina); tropical Africa and Asia.

Rhizomes suberect to erect (short-creeping to long-creeping in 2 non-Guatemalan varieties), caudex usually 1.5-3 cm. in diameter; stipes stramineous, but darkened at the base, 10-40 (55) cm. long, 1.5-5 mm. in diameter, hairy; laminae herbaceous to chartaceous, 18-55 (75) cm. long, tapering evenly to the pinnatifid apex; largest pinnae 3.5-16 cm. long, 0.8-2.0 (2.6) cm. wide, incised (0.5) 0.6-0.8 to the costae; 0-4 pairs of lower pinnae gradually reduced at the blade base; lower pinnae sometimes with small crenately lobed auricles at the superior base; segments suboblique, mostly straight, acute, or rounded; veins (4) 6-9 (11) pairs per segment, the basal pair from adjacent segments united below the sinus with an excurrent veinlet 1-2 mm. long (ours); costae and veins pubescent on both sides, the hairs often stout, 0.3-0.8 mm. long; leaf tissue pubescent below, glabrous or hairy above; stipitate yellow glands often present on both surfaces; indusia usually with dense hairs less than 0.3 mm. long; $n = 36$.

This species has often been confused with *T. dentata*, native to Africa and Asia but probably introduced in the New World (Taxon 19: 871-874. 1970).

Holttum (Kew Bull. 31: 293-339. 1976) has recently revised the Old World species of *Christella* and concluded that *Christella hispidula* (Decne.) Holtt. is the oldest name for the pantropical diploid cytotype previously known under a wide variety of names (e.g., basionyms *Dryopteris contigua* Rosenst., *Nephrodium hilsenbergii* Presl, and *Nephrodium quadrangulare* Fée). I have now seen sufficient African and Asian material to agree that it is conspecific with what I have called *Thelypteris quadrangularis* in the neotropics (Univ. Calif. Publ. Bot. 59: 1-136. 1971). The four New World varieties that I recognized previously are more or less distinct, insofar as New World material is considered, but I am uncertain of the relationship of the most widespread of them, my var. *quadrangularis* (the only variety in Guatemala) to Old World varieties. In any case, an infraspecific taxonomy of paleotropical material has not yet been attempted, so it is premature to

try to relate varieties in the two areas and thus to apply a varietal name to Guatemalan collections.

Thelypteris interrupta (Willd.) Iwatsuki, Jap. J. Bot. 38: 314. 1963. *Pteris interrupta* Willd. Phytogr. 13, t. 10. 1794. *Polypodium tottum* Thunb. Prodr. Pl. Cap. 172. 1800. *Aspidium gongylodes* Schkuhr (as "goggilodus"), Kr. Gew. 1: 193, t. 33c. 1809. *Cyclosorus gongylodes* (Schkuhr) Link, Hort. Berol. 2: 128. 1833. *Dryopteris gongylodes* (Schkuhr) O. Ktze. Rev. Gen. Pl. 2: 811. 1891. *T. gongylodes* (Schkuhr) Small, Ferns SE States 248, cum tab. 1938. *T. totta* (Thunb.) Schelpe, J. South African Bot. 29: 91. 1963. *Cyclosorus tottus* (Thunb.) Pic. Ser. Webbia 23: 173. 1968.

Marshes and swamps, 0-50 m. (and probably higher); Izabal; Petén; Santa Rosa. Southern Florida; southern Mexico; El Salvador; Honduras; Costa Rica; Panama; Antilles; South America (to northern Argentina, Paraguay). Also in the paleotropics.

Rhizomes long-creeping, black, naked, 3-6 mm. in diameter, stipe bases (1) 2-9 cm. apart, often blackened; stipes 17-105 cm. long, 3-6 mm. in diameter, glabrescent; laminae chartaceous to subcoriaceous, 30-80 cm. long, tapering evenly toward the short-pinnatifid apex; largest pinnae 7-30 cm. long, 1.0-2.2 cm. wide, incised 0.3-0.5 (0.6), lowermost short-stalked 1-4 mm.; segments deltoid, rounded or acute at the tip; veins 9-18 pairs per segment, the basal pair from adjacent segments obtusely united below the sinus with an excurrent vein usually 2-4 mm. long; scales on costae below, these tan or stramineous, glabrous or ciliate; costae, veins, and leaf tissue glabrous (ours) or pubescent (hairs 0.1-0.2 mm.) below, glabrous above except for sparse hairs less than 0.2 mm. long along costae; glands often present below, these red or orange, shining, sessile, hemispherical, most frequent on leaf tissue, along costules, and among sporangia; sori often appearing confluent when sporangia are mature; indusia glabrous (ours) or hirsute; $n = 72$ (neotropics), 36 (paleotropics).

Three neotropical varieties have usually been recognized, largely on the basis of glandularity and pubescence; their ranges are for the most part sympatric, and it seems doubtful if this variation is taxonomically significant. For the present, I prefer to recognize a single highly variable species without infraspecific divisions. All Guatemalan specimens seen are without hairs on blade and indusia.

Thelypteris kunthii (Desv.) Morton, Contr. U.S. Natl. Herb. 38: 53. 1967. *Nephrodium kunthii* Desv. Mém. Soc. Linn. Paris 6: 258. 1827. *Dryopteris normalis* C. Chr. Ark. Bot. 9 (11): 31. 1910. *T. normalis* (C. Chr.) Moxley, Bull. S. Calif. Acad. Sci. 19: 57. 1920.

Wet thickets, woods, ravines, 0-1,400 m.; Alta Verapaz; Chiquimula; Escuintla; Jalapa; Izabal; Petén; Sacatepéquez; Zacapa. Southeastern United States; eastern and southern Mexico; British Honduras; El

Salvador; Honduras; Costa Rica; Bahamas; West Indies; rare in northern South America.

Rhizomes short- to long-creeping; stipes (5) 20-80 cm. long, (1) 3-6 mm. in diameter, with basal scales castaneous, shining, lanceolate, hairy; rachises pubescent and often stipitate-glandular, usually without scales; laminae herbaceous to chartaceous, (9) 30-65 (80) cm. long, tapering evenly to the pinnatifid apex; largest pinnae basal, (2) 8-15 (20) cm. long, (0.6) 0.9-2.5 cm. broad, incised 0.6-0.8, without pronounced basal auricles; segments oblique, straight, or subfalcate, rounded or acute at the tip; veins (3) 6-11 pairs per segment, the basal pair from adjacent segments running to the sinus; scales absent on costae below; costae and veins pubescent above and below, the hairs mostly 0.2-0.5 mm. long, dense or relatively sparse, those of the costae above stouter, up to 0.8 mm. long; leaf tissue above usually lacking hairs, below hairy; light yellowish stipitate glands often present on leaf tissue and veins above and below; indusia sparsely to densely hairy, hairs 0.2-0.4 mm. long; $n = 72$.

Thelypteris ovata R. St. John var. ***lindheimeri*** (C. Chr.) A. R. Smith, Amer. Fern J. 61: 30. 1971. *Dryopteris normalis* C. Chr. var. *lindheimeri* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 182. 1913.

Uncommon, damp limestone thickets, along streams, 1,200-1,900 m. (and probably lower); Alta Verapaz; Huehuetenango. United States (central Texas); eastern and southern Mexico; British Honduras. Variety *ovata* occurs in southeastern United States and Bahamas.

Rhizomes creeping; fronds (30) 55-135 (165) cm. long, tapering evenly toward the pinnatifid apex; stipes about as long as blades, (1.5) 2-6 mm. in diameter, the scales at the base linear-lanceolate, tan to brown, ciliate; rachises with a few similar tan scales; largest pinnae (5) 10-25 cm. long, 0.8-2.2 cm. wide, incised more than 0.8; lowermost pinnae the longest, often somewhat narrowed toward their base; basal segments of medial pinnae often narrower and slightly longer than more distal segments, often parallel to rachis; segments oblique, subfalcate; veins 6-13 pairs per segment, lowermost reaching the margin at or just above the sinus; tan scales 0.5-1.5 mm. long on costae below; costae, veins, and leaf tissue pubescent below (hairs mostly 0.2-0.5 mm. long), glabrous above except along the costae; sori supramedial to submarginal; indusia with hairs mostly 0.2-0.4 mm. long; paraphyses lacking; spores 31-42 (47) μ m. long; $n = 36$.

Thelypteris patens (Swartz) Small, Ferns SE States 243. 1938. *Polypodium patens* Swartz, Prodr. 133. 1788. *Dryopteris patens* (Swartz) O. Ktze. Rev. Gen. Pl. 2: 813. 1891.

Wet mixed forests, thickets, ravines, stream banks, 0-1,600 m.; Alta Verapaz; Baja Verapaz; Escuintla; Izabal; Petén; Quezaltenango; Retalhuleu; Santa Rosa; Zacapa. Florida; southern Mexico; British Honduras; Honduras and El Salvador to Panama; Antilles; South America (to northern Argentina).

Rhizomes erect, caudex 2-4 cm. thick, apex and stipe bases covered with large ovate, tan (whitish when young) scales up to 1.5×0.5 cm., with cells isodiametric; stipes (5)

15-50 (95) cm. long, (1) 2.5-9 (12) mm. in diameter; laminae (8) 25-75 (100) cm. long, tapering evenly toward the apex; largest pinnae (lowest or next to lowest) (3) 10-32 cm. long, (0.5) 1.2-3.0 (4.0) cm. wide (excluding basal segments, which may be elongated parallel to rachis or pinnatifid auricles to 5 cm. long), usually deeply incised 0.7-0.9 their width; segments oblique, subfalcate to falcate, acute; veins (6) 8-14 (21) pairs per segment, the basal pair from adjacent segments running to the sinus; scales absent on costae; costae, veins, and lamina below pubescent and often with short-stipitate glands, sometimes sparsely hairy (rarely glabrous), above glabrous except along the costae, the hairs mostly 0.2-0.4 mm. long; indusia tan, often with short-stipitate glands, pubescent to sparsely hairy; $n = 36, 72$.

The commonest variety (and the only one occurring in Guatemala) is var. *patens*. Two other varieties of this widespread species occur in the neotropics, one in southern Brazil and adjacent countries and the other widespread from the Antilles through much of South America, with a few collections from Central America. *Thelypteris patens* usually occurs at lower elevations than does *T. puberula*, also common and sometimes confused with *T. patens*.

Thelypteris puberula (Baker) Morton, Amer. Fern J. 48: 138. 1958. *Nephrodium puberulum* Baker in Hook. & Bak. Syn. Fil. ed. 2. 495. 1874. *Dryopteris puberula* (Baker) O. Ktze. Rev. Gen. Pl. 2: 813. 1891. *D. feei* C. Chr. Index. Fil. 264. 1905. *D. augescens* (Link) C. Chr. var. *puberula* (Baker) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 184. 1913.

Along streams, wet forests and thickets, ravines, 1,200-2,500 m.; Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; El Quiché; Guatemala; Huehuetenango; Sacatepéquez; San Marcos; Sololá. Southwestern United States; throughout Mexico (type from Veracruz, near Huatusco, *Schaffner 247* in part) El Salvador; Honduras; Costa Rica.

Rhizomes creeping, stipe bases (0.5) 1-3 cm. apart; stipes equaling blades, 15-50 (80) cm. long, (2) 3-7 mm. in diameter, paleate at the base, the scales hairy, not persistent; laminae chartaceous to subcoriaceous, 20-55 (85) cm. long, tapering evenly toward the pinnatifid apex, or the laminae abruptly reduced just below the somewhat elongate apex; largest pinnae the lowest, 7-20 (26) cm. long, 0.9-2.0 (3.0) cm. wide; incised 0.5-0.8 their width; lower several pairs of pinnae narrowed toward their base except for a slightly enlarged entire acroscopic basal segment; basal basiscopic segment of distal pinnae strongly adnate to rachis; segments oblique, subfalcate, acutish; veins 7-12 (15) pairs per segment, the basal pair (or 2-3 pairs) from adjacent segments connivent at the sinus; costae below with a few minute castaneous scales less than 0.5 mm. long; costae, veins, and leaf tissue pubescent below (hairs ca. 0.2 mm. long), eglandular or sparsely glandular, glabrous above except along the costae; indusia hairy; $n = 72$.

All Guatemalan material is referable to var. *puberula*; variety *sonorensis*, with short-pubescent lamina above, is confined to western Mexico and southwestern United States. Hybrids between *T. puberula* and other species in subg. *Cyclosorus* occur infrequently in Mexico

and Guatemala, e.g., *Williams et al.* 41516 (F), which has nearly 100 percent malformed spores and failure of many sporangia to mature spores at all.

Thelypteris tuerckheimii (Donn.-Sm.) Reed, *Phytologia* 17: 321. 1968. *Nephrodium tuerckheimii* Donn.-Sm. Bot. Gaz. (Crawfordsville) 12: 133, t. 11. 1887. *Dryopteris tuerckheimii* (Donn.-Sm.) C. Chr. Index Fil. 299. 1905.

Wet mixed forest, moist banks, 1,200-2,000 m.; Alta Verapaz (type from near Cobán, *Tuerckheim s.n.*, ed. Donn.-Sm. 704); El Progreso; Huehuetenango. Mexico (Chiapas).

Rhizomes stout, creeping; stipes 30-85 cm. long, 4-10 mm. in diameter at the base, densely clothed with brown or light-brown ovate-lanceolate scales up to 10 mm. long, scales glabrous; rachises pubescent, moderately but still conspicuously paleaceous, the scales like those of the stipe but smaller; blades coriaceous to subcoriaceous, (30) 45-90 cm. long, (16) 25-55 cm. wide, tapering evenly toward the short-pinnatifid apex; largest pinnae basal, (8) 12-28 cm. long, 1.3-3.0 cm. broad, incised ca. 0.7-0.8 of the way to the costae, often strongly auricled at the base; segments subfalcate, the margins often strongly revolute; veins 10-18 pairs per segment, the basal ones connivent to the sinus; scales present on costae and costules below; costae, veins, leaf tissue, and the persistent indusia rather densely pubescent below, the hairs mostly 0.3-0.5 mm. long; $n = 36$.

Collections from outside Alta Verapaz are somewhat less scaly on the stipes and rachises and resemble somewhat specimens of *T. ovata* var. *lindheimeri*. *Thelypteris tuerckheimii* has usually been collected in limestone regions.

THELYPTERIS subg. **GONIOPTERIS** (Presl) Duek, *Adansonia*, ser. 2. 11: 720. 1971. *Goniopteris* Presl, Tent. Pterid. 181. 1836. *Dryopteris* subgenus *Goniopteris* (Presl) C. Chr. Index Fil. XXII. 1906. *Thelypteris* sect. *Goniopteris* (Presl) Morton, Amer. Fern J. 53: 154. 1963.

Rhizomes with numerous thick proplike roots ca. 1 mm. in diameter, these seemingly glabrous; rhizome apex and stipe base scales few, usually beset with minute forked or stellate hairs ca. 0.1 mm. long; fronds rarely simple, mostly pinnate or pinnate-pinnatifid, gradually reduced toward the pinnatifid apex or with a conform terminal pinna; gemmiparous buds sometimes present in axils of distal pinnae; lowermost pinnae the longest or nearly so, rarely reduced; axes and leaf tissue, especially abaxially, with few to many stellate or forked hairs, also with acicular hairs, rarely with only acicular hairs (*T. ghiesbreghtii*); aerophores absent; leaf tissue dark green or gray-green, sometimes verruculose; veins connivent at the sinus, or with 1 to several pairs of veins united below the sinus, rarely free; indusia present or absent, often minute and easily overlooked; sporangia glabrous or often setose with acicular or stellate hairs; $x = 36$.

Restricted to New World tropics and subtropics, from Florida, Antilles, and central Mexico to Bolivia and northeastern Argentina.

Subgenus *Goniopteris* is primarily a group of low- to middle-elevation rain forests, with species becoming rare above 1,500 m. and nonexistent above 2,000 m.; altogether there are perhaps 75 species, 18 in Guatemala.

- a. Veins meniscioid, i.e., 3 or more pairs of veins from adjacent segments anastomosing with an excurrent vein that ends before reaching the next pair of anastomosing veins.
- b. Blades ternate, i.e., with 1 pair of lateral pinnae and a terminal pinna; sporangia setose. *T. meniscioides* var. *ternata*.
- b. Blades with 2 or more pairs of lateral pinnae; sporangia glabrous or setose.
- c. Sporangial walls with several short setae; meniscioid veins 3- to 5-seriate; costae below moderately hairy, hairs mostly 0.2-0.4 mm. long. *T. poiteana*.
- c. Sporangial walls glabrous (rarely with a few minute setae in *T. meniscioides*); meniscioid veins 7- to 12-seriate.
- d. Costae, veins, and leaf tissue moderately to densely hairy below, the hairs up to 1.5 mm. long, with many hairs ca. 1.0 mm. long. *T. ghiesbreghtii*.
- d. Costae, veins, and leaf tissue glabrous or nearly so below, hairs if present less than 0.2 mm. long. *T. meniscioides*.
- a. Veins free, or connivent at the sinus, or the lower 1-2 (3) pair(s) united with an excurrent vein to the sinus.
- e. Fronds with 2 or fewer free pinnae below, the rest of the lamina pinnatifid; fronds less than 30 cm. long. *T. skinneri*.
- e. Fronds with 3 or more free pinnae; fronds usually greater than 30 cm. long.
- f. Fronds arching, radicant at or near the tip and producing new fronds; pinnae 2.5 cm. long or less, entire to lobed ca. 0.25 their width. *T. reptans*.
- f. Fronds not rooting at the tip (a few species producing rachis buds back from the tip); pinnae greater than 2.5 cm. long, shallowly to deeply lobed more than 0.75 their width.
- g. Laminae with a terminal pinna resembling the lateral ones; sporangia with or without minute setae or furcate hairs.
- h. Sori supramedial to submarginal; indusia persistent and relatively large. *T. paucipinnata*.
- h. Sori subcostular to supramedial; indusia absent or minute and easily overlooked.
- i. Pinnae serrulate to lobed $\frac{1}{4}$ to the costae, cuneate at the base; basal veins upcurved and anastomosing under acute angles, the following pairs usually also anastomosing. *T. obliterated*.
- i. Pinnae incised 0.5-0.8 to the costae, truncate or cuneate at the base; only basal pair of veins anastomosing at an obtuse angle, or veins connivent at the sinus.
- j. Rachis, costae, costules, and veins below glabrous. ... *T. toganetra*.
- j. Rachis, costae, costules, and often veins below sparsely to densely hairy.
- k. Lowermost veins united at an obtuse angle with an excurrent vein to the sinus; sporangia setose. *T. tetragona*.
- k. Lowermost pairs of veins from adjacent segments connivent at the sinus; sporangia glabrous or setose.
- l. Sporangia minutely furcate- or stellate-hairy; costae below with short stellate hairs and also long, stout, acicular hairs. *T. praetermissa*.

- l. Sporangia glabrous or setulose; costae below with mostly short simple hairs, without long, stout acicular hairs.
 - m. Pinnae mostly stalked 1-3 mm.; lowermost pinnae with a cuneate or sinuate base. *T. minor*.
 - m. Pinnae sessile or nearly so; lowermost pinnae truncate at their base; not narrowed. *T. imbricata*.
- g. Laminae without a distinct terminal pinna, upward gradually narrowed into a pinnatifid apex; sporangia glabrous (sometimes hairy in *T. asterothrix*).
- n. Costae and sometimes veins and leaf tissue below with rather dense stellate or furcate hairs.
 - o. Fronds small, less than 45 cm. long; indusia absent; stellate hairs all stalked.
 - p. Lowermost pair of veins from adjacent segments united below the sinus with excurrent vein to sinus. *T. asterothrix*.
 - p. Lowermost pair of veins from adjacent segments meeting margin at the sinus. *T. stolzeana*.
 - o. Fronds greater than 45 cm. long; indusia absent or present (small); stellate hairs on leaf tissue often sessile.
 - q. Some hairs on costae and leaf tissue below anchor-shaped, *i.e.*, with 2 short recurved branches at the tip. *T. biolleyi*.
 - q. Anchor-shaped hairs absent below. *T. hatchii*.
- n. Costae, veins, and leaf tissue glabrous or with unbranched hairs below.
 - r. Pinnae less than 7 cm. long, often less than 5 cm. long; indusia absent; without rachis buds. *T. blanda*.
 - r. Pinnae usually greater than 7 cm. long (except *T. schippii*); indusia present, but small; rachis buds usually present.
 - s. Pinnae lobed ca. $\frac{1}{3}$ their width; lowermost veins united or connivent below the sinus. *T. schippii*.
 - s. Pinnae lobed ca. 0.7 their width; veins meeting margin at the sinus, but not connivent. *T. resiliens*.

Thelypteris asterothrix (Fée) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 57. 1953. *Goniopteris asterothrix* Fée, Gen. Fil. 253. 1852. *Dryopteris asterothrix* (Fée) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 221, f. 29. 1913. *D. malacothrix* Maxon, Proc. Biol. Soc. Wash. 43: 87. 1930.

Uncommon, bluffs, 300-500 m.; Alta Verapaz; Izabal? Costa Rica; Venezuela; Cuba; Jamaica; Hispaniola.

Rhizomes short-creeping to suberect; stipes mostly 5-18 cm. long and less than 1 mm. in diameter, with patent stout acicular hairs (ca. 1 mm.) and short stellate hairs (0.1-0.2 mm.); laminae to ca. 15 cm. long, 4-6 cm. broad; pinnae 5-10 pairs, the lowermost short-stalked (1-2 mm.) and sometimes slightly reduced, the upper sessile, ultimately confluent into a pinnatifid apex, 0.9-1.5 cm. broad, rounded at apex, incised ca. $\frac{1}{2}$ the way to the costae; segments 3-4 mm. broad, rounded at apex; veins 3-4 (6) pairs per segment, lower pair from adjacent segments united below sinus with excurrent vein to the sinus; costae, costules, veins, and leaf tissue on both sides with stalked 2- to 4-branched or forked hairs, the veins and costae with a few longer, stout acicular hairs;

sori medial, exindusiate; receptacle with numerous stalked stellate hairs; sporangia glabrous or bearing 2-3 erect furcate or stellate hairs; $n = 72$.

Closely related to *T. reptans*, but distinguished by its nonproliferous, somewhat broader fronds with fewer pairs of pinnae.

Thelypteris biolleyi (Christ) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 58. 1953. *Aspidium biolleyi* Christ in Pittier, Prim. Fl. Costaric. 3: 31. 1901. *Dryopteris nephrodoides* (Kl.) Hieron. var. *biolleyi* (Christ) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 248. 1913.

Uncommon, rain forests, 350-550 m.; Alta Verapaz; Quezaltenango. Southern Mexico; Honduras; Costa Rica; Panama; Jamaica; Colombia to Peru, Brazil.

Rhizomes short-creeping to suberect; stipes up to 50 cm. long or more, brownish, stellate-pubescent; laminae to 75 cm. long with a pinnatifid apex; pinnae to 22 (28) cm. long, 3 (4) cm. broad, sessile or short-stalked up to 1 mm., incised ca. 0.5-0.7 their width, lower pinnae narrowed at their subcuneate base; segments suboblique, subfalcate, rounded at the apex, ca. 6 mm. broad; veins up to 16 pairs per segment, the lowermost pair from adjacent segments anastomosing at a 60-90° angle, with an excurrent vein; costae, costules, and leaf tissue below with numerous anchor-shaped hairs 0.2-0.5 mm. long (2 recurved branches at the tip), also with a few sessile, appressed, stellate hairs (4 arms), these especially evident along the excurrent veins; axes above with mostly acicular hairs 0.2-0.5 mm. long, leaf tissue above with numerous, appressed, stellate hairs; leaf tissue dark green, herbaceous, verruculose; sori inframedial to medial, exindusiate or with a minute indusium; sporangia glabrous or with a few minute stellate hairs; $n = 36$.

Thelypteris blanda (Fée) Reed, Phytologia 17: 264. 1968. *Phegopteris blanda* Fée, Mém. Fam. Foug. 8: 91. 1857. (Type from Mexico, Veracruz, Mirador, Schaffner 222.) *Phegopteris caespitosa* Fourn. Mex. Pl. 1: 89. 1872. *Dryopteris blanda* (Fée) C. Chr. Index Fil. 254. 1905. *D. caespitosa* (Fourn.) C. Chr. Index Fil. 256. 1905.

Limestone rocks, stream banks, forested ravines, 50-1,400 m.; Alta Verapaz; Izabal; Petén; Quezaltenango; Suchitepéquez. British Honduras; southern Mexico (Hidalgo to Oaxaca, Chiapas); Costa Rica.

Rhizomes erect to suberect; stipes (8) 15-20 (25) cm. long, ca. 1 mm. in diameter, stramineous or darkened, glabrous; rachises with a few stellate hairs ca. 0.1 mm. long, glabrescent, without buds; laminae pinnate-pinnatifid, ovate-lanceolate, 12-25 cm. long, 7-10 (15) cm. broad, gradually reduced to a pinnatifid apex; pinnae 7-12 pairs, sessile, up to 7.5 cm. long, 1.5 (2.0) cm. broad, the lowermost pair somewhat shortened and deflexed, deeply incised to within 1 mm. of costae; segments 7-15 pairs per pinna, oblique, obtuse or acutish at the apex; veins 5-6 pairs per segment, lowermost reaching the margin well above the sinus; costae on both sides sparsely pubescent by acicular hairs 0.2-0.4 mm. long; leaf tissue herbaceous, thin, dark green, glabrous, not verruculose; sori inframedial to medial, exindusiate; sporangia glabrous; $n = 36$.

Thelypteris ghiesbreghtii (Hook.) Morton, Contr. U.S. Natl. Herb. 38: 45. 1967. *Goniopteris mollis* Fée, Gen. Fil. 252. 1852. *Polypodium crenatum* Swartz var. *ghiesbreghtii* Hook. Sp. Fil. 5: 3. 1864. *Dryopteris ghiesbreghtii* (Hook.) C. Chr. Index Fil. 267. 1905. *D. mollis* (Fée) Maxon, Contr. U.S. Natl. Herb. 13: 18. 1909 (not *D. mollis* [Jacq.] Hieron, 1907).

Wet forests, cafetals, near sea level to 700 m.; Alta Verapaz; Izabal; San Marcos. Mexico (Chiapas, type from Tabasco, Teapa, *Linden 1499*); Nicaragua; Costa Rica; Panama.

Rhizomes creeping; stipes 30-40 cm. long, scaleless or sparingly scaly; laminae (15) 30-50 cm. long, up to 30 cm. broad, simply pinnate; pinnae 2-5 sessile lateral pairs and a conform terminal one, 20-30 cm. long, 4.5-8 cm. broad, elliptic, with an acuminate tip, irregularly serrulate or lobed, without buds in the axils; veins 10-12 pairs, 7-12 pairs meniscioid, the uppermost pairs anastomosing at obtuse angles; leaf tissue and veins densely soft-hairy beneath, the hairs up to 1.5 mm. long, often ca. 1.0 mm. long, furcate and stellate hairs apparently lacking throughout; sori in a double row between the costules, exindusiate or with very small indusial remnant; sporangia glabrous but intermixed with long hairs from the receptacle; $n = 36$.

This is the only species of subg. *Goniopteris* that apparently lacks stellate or forked hairs. However, on the basis of other characters and its obvious affinities to *T. poiteana* it is clearly a member of the subgenus. It has often been collected in coffee and cacao plantations.

A very atypical collection, which may represent an undescribed species, is *Steyermark 39161*. It differs from all other specimens of *T. ghiesbreghtii* in the much shorter pubescence, but is apparently closest to *T. ghiesbreghtii* on the basis of its similar venation and fragmentary indusium.

Thelypteris hatchii A. R. Smith, Amer. Fern J. 63: 118, *f.* 1-3. 1973.

Uncommon, wet forests, ca. 1,000 m.; Alta Verapaz (type from Senahu, Cerro Sillab, *Hatch & Wilson 159*, US). Southern Mexico; Costa Rica.

Rhizomes erect or suberect; stipes brownish, 20-45 cm. long, puberulous, the hairs stellate, ca. 0.1 mm. long; laminae dark green, 30-50 cm. long, with a hastate terminal segment; pinnae 9-14 pairs, sessile or the lowermost with a stalk less than 1 mm.; largest pinnae up to 20 cm. long, 2.7 cm. wide, incised ca. 0.5-0.6; lowermost 2-3 pairs of pinnae reflexed and slightly narrowed toward their base, slightly shortened; segments sub-oblique, subfalcate, ca. 5 mm. broad, rounded at the tip; veins 9-12 pairs per segment, the basal pair from adjacent segments connivent at the sinus, or anastomosing at an acute angle below the sinus; rachises, costae, veins, and leaf tissue with stellate or furcate hairs 0.1-0.2 mm. long, these densest along the costae and rachis, a few longer acicular hairs also present especially along the veins and costae above; sori medial to

supramedial, with a small but persistent indusium; indusia with simple or furcate hairs 0.1 mm. long; sporangia glabrous; $n = 36$.

Thelypteris imbricata (Liebm.) Reed, *Phytologia* 17: 284. 1968. *Polypodium imbricatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 210. 1849.

Wet woods and barrancas, often near streams, 300-1,000 m.; Quezaltenango; Retalhuleu; Sololá; Suchitepéquez. Southern Mexico; Costa Rica.

With the characters of *T. tetragona*, but differing from that in having the lowermost pair of veins from adjacent segments connivent at the sinus, or sometimes arcuately and acutely united just below the sinus; sporangia glabrous; spores relatively small, ca. 25-40 μ m long (perispore excluded); apparently diploid, $n = 36$.

This species is a problematic one in that it is not always easy to separate from *T. tetragona*. All of the Guatemalan collections of *T. imbricata* are from the Pacific slope, while *T. tetragona* is very common on the Atlantic slope but uncommon on the Pacific slope. Apparently, both species occur in Dept. Retalhuleu, and there are a few specimens that suggest hybridization is taking place (see *T. tetragona* for a discussion of these). Several specimens I tentatively place under *T. imbricata* are sterile, and so cannot be evaluated for one of the important key characters. Additional cytotaxonomic study is needed to clarify the relationships of *T. tetragona*, *T. imbricata*, *T. minor*, and *T. toganetra*, all closely related.

Thelypteris meniscioides (Liebm.) Reed, *Phytologia* 17: 292. 1968. *Polypodium meniscioides* Liebm. Kongel. Danske Vidensk. Selsk. Skr. Naturv. Afd. V. 1: 211. 1849. *Dryopteris meniscioides* (Liebm.) C. Chr. Index Fil. 277. 1905. *D. liebmannii* Maxon & Morton, Bull. Torrey Bot. Club 65: 348. 1938.

Uncommon, wet limestone forests, stream banks, lower elevations, 900 m. (and probably lower); Alta Verapaz; Izabal. Southern Mexico (type from Oaxaca, *Liebmann*, C).

Rhizomes short-creeping; stipes ca. 5-7 mm. in diameter, 30-60 cm. long, glabrous; laminae 25-35 cm. long, nearly as broad; pinnae (3) 4-12 lateral pairs and a conform terminal one, narrowed on both sides of the middle, 15-20 cm. long, 3.5-5.0 cm. broad, the margin entire, crenate, or very shallowly lobed, long-acuminate at the tip; costules ca. 4-5 mm. apart, with 8-10 pairs of veins, these meniscoid; costae, veins, and leaf tissue glabrous or nearly so above and below, or with a few minute furcate hairs (0.1 mm. long) toward the bases of costae below; leaf tissue chartaceous to subcoriaceous; sori in double rows between the costules, exindusiate; sporangia glabrous, rarely minutely setulose, the setae less than 0.1 mm. long; $n = 36$.

Thelypteris meniscioides* var. *ternata A. R. Smith, *Phytologia* 34: 232. 1976.

Wet limestone forests, on rocks, 0-900 m.; Alta Verapaz; Izabal (type along Río Frío, *Steyermark 41644*, F).

Differs from var. *meniscioides* in the blades usually ternate, with 1 (3) pair(s) of lateral pinnae, and in having sporangia always setose-hairy (hairs 0.1 mm. long).

Possibly more common than the type variety in Guatemala.

Thelypteris minor (C. Chr.) A. R. Smith, *Phytologia* 34: 232. 1976. *Dryopteris nicaraguensis* (Fourn.) C. Chr. var. *minor* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 252. 1913.

Common, wet forests, along trails, 100-1,200 m.; Alta Verapaz (lectotype from Secanquin, *Maxon & Hay 3196* [US], chosen by Smith, *Phytologia* 34: 232. 1976); Chiquimula; Izabal; Petén; Santa Rosa. El Salvador; Costa Rica.

Rhizomes suberect to erect, caudex 1.5-2 cm. in diameter, to 10 cm. long; fronds mostly 60-80 cm. long, with stipes brownish, 2-4 mm. wide, as long as or slightly longer than laminae; pinnae 8-10 pairs (with a nearly conform terminal pinna), 12-16 (20) cm. long, 2.0-2.8 cm. broad, incised 0.5-0.6 (0.7) of the way to costae, all but the uppermost stalked 1-3 mm.; segments oblique, subfalcate, 4-6 mm. broad, acutish to obtuse at the tip, the basal 1-3 pairs on lowermost 3-5 pairs of pinnae rather abruptly shortened (to a sinuate wing on lowermost 1-2 pairs of pinnae); veins 10-12 (15) pairs per segment, the lowermost 2 pairs connivent at the sinus or (less frequently) united at an acute angle below the sinus; costae below with scattered to dense hairs 0.1 mm. long, these mostly acicular but a few furcate; leaf tissue dark green, chartaceous, glabrous on both sides; sori inframedial; sporangia usually setulose, with hairs 0.1 mm. long, occasionally glabrous; exindusiate.

Thelypteris oblitterata (Swartz) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 62. 1953. *Polypodium oblitteratum* Swartz, Prodr. 132. 1788. *Dryopteris oblitterata* (Swartz) C. Chr. Index Fil. 280. 1905.

Wet forests, ditches, at low elevations, near sea level to 500 m.; Izabal; Petén. Southern Mexico; British Honduras; Honduras; Costa Rica; Cuba; Jamaica (type); Hispaniola.

Rhizomes short-creeping; stipes (32) 40-50 cm. long, stramineous to tan, \pm glabrous; rachises pubescent with stellate hairs ca. 0.1 mm. long, without buds; laminae pinnate, up to 50 cm. long, 40 cm. broad, with a conform terminal pinna; pinnae (4) 5-10 pairs, stalked up to 5 mm., alternate, 12-20 cm. long, (1.3) 2.0-3.5 cm. broad, sharply serrate (the teeth oblique, acute) or shallowly lobed up to $\frac{1}{2}$ their width, the lower pinnae narrowed toward their entire cuneate or rounded base; veins 6-8 (11) pairs, the lower 2 pairs anastomosing with an excurrent branch to the sinus, to which the next 2-3 pairs of veins are connivent; costae below puberulous with simple (a few stellate) hairs 0.1 mm. long; leaf tissue above and below glabrous, chartaceous to subcoriaceous; sori exindusiate, in 2 convergent rows, the lower ones medial, the upper ones subcostular; sporangia with a few simple setae 0.1 mm. long; $2n = 108$ (apogamous?).

A putative hybrid between this species and *T. praetermissa* has been collected in British Honduras: *Gentle 6120* (F, NY, UC, US). The

hybrid is intermediate between its supposed parents and has nearly 100 percent malformed spores.

Thelypteris paucipinnata (Donn.-Sm.) Reed, *Phytologia* 17: 302. 1968. *Nephrodium fendleri* (D.C. Eaton) Hook. var. *paucipinnatum* Donn.-Sm. Bot. Gaz. (Crawfordsville) 12: 134. 1887. *Dryopteris paucipinnata* (Donn.-Sm.) Maxon, Contr. U.S. Natl. Herb. 13: 19. 1909.

Locally common along streams, wet forests, near sea level to 1,400 m.; Alta Verapaz (lectotype from Petén, *Tuerckheim s.n.* [ed. Donn.-Sm. 767] US, chosen by Maxon, *tom. cit.* 20); Baja Verapaz; Izabal. Southern Mexico; British Honduras.

Rhizomes creeping to suberect; stipes darkened, ca. (35) 65 cm. long, glabrous except for a few deciduous basal scales; rachises usually with buds in axils of upper pinnae; laminae 45-50 cm. long, ca. 25 cm. broad, with (3) 5-8 (10) pairs of lateral pinnae and a conform terminal one, all about the same size; pinnae (17) 20-25 cm. long, ca. 3 (4) cm. broad at the middle, falcate, obliquely pinnatifid ca. $\frac{1}{2}$ their width, tapering gradually to a narrow entire long-acuminate apex, at the base narrowly cuneate, stalked up to 8 mm.; veins ca. 10-14 pairs per segment, 4-6 lowermost pairs from adjacent segments connivent at the sinus, occasionally the lowest pairs united below the sinus; leaf tissue chartaceous to subcoriaceous, verruculose below; sori submarginal; indusia whitish, reniform, persistent; sporangia glabrous.

Thelypteris poiteana (Bory) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 63. 1953. *Polypodium crenatum* Swartz, Prodr. 132. 1788 (*non* Forssk. 1775). *Lastrea poiteana* Bory, Dict. Class. 9: 233. 1825. *Dryopteris poiteana* (Bory) Urban, Symb. Antill. 4: 20. 1903. *Goniopteris poiteana* (Bory) Ching, *Sunyatsenia* 5: 239. 1940.

Wet forested ravines, 200-350 m.; Alta Verapaz; Izabal; San Marcos; Santa Rosa. Southern Mexico; British Honduras to Panama; Antilles; Colombia to northern Brazil, Peru.

Rhizomes short-creeping, ca. 1 cm. in diameter; fronds few, 0.5-1 m. long; stipes glabrescent; laminae 20-40 cm. long, 18-30 cm. broad, 1-pinnate; pinnae 2-6 lateral pairs and a conform terminal one, 12-22 cm. long, 3-6 cm. broad, subentire or crenate or coarsely serrate, rarely shallowly lobed, sometimes gemmiparous in the axil; basal pinnae mostly short-stalked, subcuneate at the base, those above sessile and rounded; costules 4-8 mm. apart; veins meniscoid, with 6-9 pairs of secondary veins, the lower 3-5 pairs upcurved and acutely united with a free excurrent veinlet, usually the next few pairs alternately united in a common veinlet running to the sinus; costae, veins, and leaf tissue below pilose, the hairs mostly acicular, ca. 0.3 (1.0) mm. long; sori in a double row between the costules, exindusiate; sporangia with 4-6 acicular setae 0.1-0.3 mm. long; $n = 72$.

Thelypteris praetermissa (Maxon) A. R. Smith, *Phytologia* 34: 232. 1976. *Dryopteris praetermissa* Maxon, Proc. Biol. Soc. Wash. 57: 20. 1944.

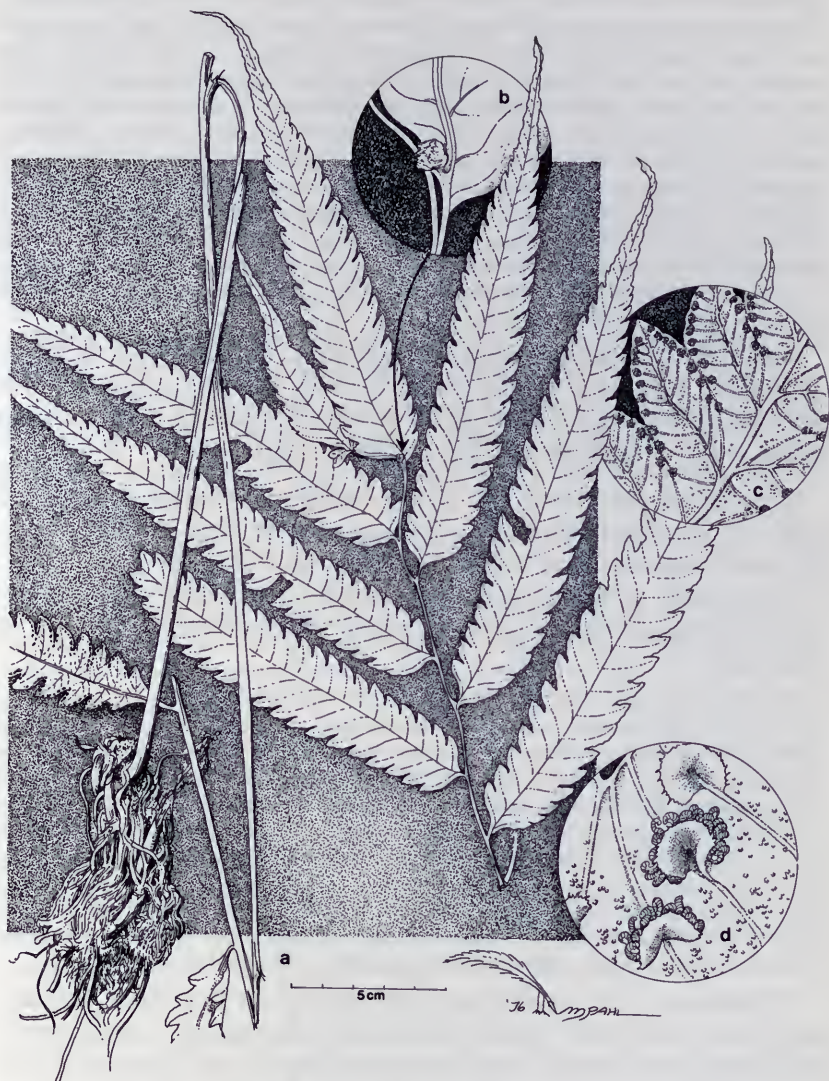


FIG. 76. *Thelypteris* subgenus *Goniopteris*. *T. paucipinnata*. a, habit, $\times \frac{1}{2}$; b, bud at base of distal pinna, $\times 1\frac{1}{2}$; c, portion of fertile pinna, showing venation and sori, $\times 2$; d, sori, greatly magnified.

Tropical rain forests, low elevation; Petén. British Honduras (type from El Cayo District, *Bartlett 13104*, MICH); Honduras; Nicaragua.

Rhizomes suberect, caudex 2-3 cm. in diameter; fronds to 1.3 m. long, with stipes nearly equaling the lamina; stipes puberulous with stellate hairs ca. 0.1 mm. long; laminae to 60 cm. long, 50 cm. broad; pinnae 8-12 pairs with a terminal pinna, 20-25 cm. long, 2-4 cm. broad, stalked 2-5 mm., apex long-attenuate; lowermost pinnae with the base abruptly sinuate-cuneate, lobed ca. $\frac{2}{3}$ their width; segments oblong, subfalcate, obtuse or acutish at the apex, ca. 5-7 mm. between costules; veins 10-16 pairs per segment, the basal 3-4 pairs running to a sinus membrane; costae beneath with stalked stellate hairs mostly 0.1-0.3 mm. long with 2-6 spreading or recurved arms, also with some longer, stiffer, acicular hairs ca. 1 mm. long; costules and veins beneath with similar, but less numerous and shorter, hairs; leaf tissue glabrous on both sides, chartaceous; sori inframedial to medial, exindusiate, the sporangia bearing numerous very thin furcate or stellate hairs 0.1 mm. long.

A single Guatemalan collection from Petén (*Contreras 5462*, F) is somewhat doubtfully referred here. It differs from the typical form primarily in having the lowest pair of veins obtusely united below the sinus, and in sporangial hairs mostly unbranched.

Thelypteris reptans (J. F. Gmel.) Morton, *Fieldiana*, Bot. 28: 12. 1951. *Polypodium reptans* J. F. Gmel. *Syst. Nat.* 2: 1309. 1791. *Dryopteris reptans* (J. F. Gmel.) C. Chr. *Index Fil.* 288. 1905.

Uncommon, on bluffs and limestone rocks, 1,000-1,400 m.; Alta Verapaz; Huehuetenango. Florida; southern Mexico; Antilles; Bahamas; Venezuela.

Rhizomes small, decumbent to suberect; fronds usually numerous, laxly arching or procumbent, subdimorphic, the sterile often rooting at the attenuate tip or along the rachis, (10) 15-50 (90) cm. long, fertile more erect and longer stalked, not rooting at the tip; laminae mostly 10-30 cm. long, 3-5 (10) cm. broad, pinnate in the lower half or throughout; pinnae stalked ca. 1 mm. or sessile, entire to crenate to shallowly lobed to ca. $\frac{1}{2}$ their width, linear to oblong or oval, truncate or sometimes subcordate at the base (fertile pinnae usually entire and more linear than sterile ones); veins 2-5 (7) pairs per segment, the basal pair usually united, with an excurrent branch to the sinus, or veins free; costae, veins, and leaf tissue minutely stellate-pubescent or furcate-hairy on both sides, also with simple hairs; indusia absent or very small, bearing a few long simple hairs and/or forked hairs; sporangia deciduously stellate-hairy; $n = 36, 72$.

Christensen (1913) recognized four varieties of *Dryopteris reptans*, but these seem only weakly distinguishable and are possibly only growth forms. Material I have seen from Mexico and Guatemala is as uniform as can be expected where leaves of a single plant are often extremely polymorphic.

Thelypteris resiliens (Maxon) A. R. Smith, *Amer. Fern J.* 63: 121. 1973. *Dryopteris resiliens* Maxon, *Field Mus. Nat. Hist. Bot. Ser.* 17: 302. 1938.

Uncommon, known from Guatemala by a single collection (*Steyermark 39159*, F), 50-100 m.; Izabal. Mexico (Chiapas); Honduras (type).

Rhizomes creeping to suberect, ca. 1 cm. in diameter; rhizome scales few, 3-5 mm. long, tan, glabrous; fronds subfasciculate, 40-70 cm. long, the stipes about as long as the blades, stramineous, stellate-hairy; laminae pinnate-pinnatifid, 20-35 cm. long, 12-20 cm. broad, lanceolate to ovate-lanceolate, gradually reduced toward the pinnatifid apex; pinnae 15-19 pairs, sessile, 2-3 lowermost pairs deflexed, these the largest, 8-12 cm. long, 1.4-3.0 cm. broad, pinnatifid ca. 0.7 to the costae; ultimate segments oblique, subfalcate, 4-5 mm. between costules, acutish at the apex; one or more upper pinnae gemmiparous at the base; veins 10-13 pairs, the basal pairs running nearly or quite to the sinus, but not connivent; costae and costules puberulous below, the hairs mostly simple (a few stellate), ca. 0.1 mm. long; leaf tissue herbaceous, verruculose throughout, glabrous; sori medial; indusia small, tan, ciliolate, persistent; sporangia glabrous.

Thelypteris schippii (Weatherby) A. R. Smith, *Phytologia* 34: 233. 1976. *Dryopteris schippii* Weatherby, *Amer. Fern J.* 25: 52. 1935.

Uncommon along shady banks, low elevations; known only from British Honduras, Toledo District (Type: Machaca Creek, *Schipp 8-782*, GH). In addition to two collections cited by Weatherby, a third collection is *Gentle 5072* (UC).

Rhizomes suberect to erect; fronds 35-75 cm. long, with stipes 0.5 (sterile fronds) to ca. 1.0 times as long as laminae; stipes grayish-brown, stellate-puberulent distally; rachises densely stellate-puberulent and with longer acicular hairs intermixed, toward the apex proliferous; laminae chartaceous to subcoriaceous, 17-33 cm. long, with a long-pinnatifid apex; pinnae 7-11 pairs, the largest the lowest or next lowest, lobed ca. $\frac{1}{4}$, cuneate at the base on the lower side, rounded, subtruncate or somewhat auricled on the upper, rather abruptly narrowed near the obtuse apex; medial pinnae 4-7 cm. long, 1.3-1.8 (2.5 in sterile fronds) cm. broad, distal pinnae becoming less deeply lobed, ultimately subentire; segments obtuse, 4-5 mm. broad, suboblique, straight or subfalcate; veins 4-6 pairs, the basal pair from adjacent segments united or connivent below the sinus; costae below with both simple and stellate hairs, above with simple hairs; veins and leaf tissue below glabrous or sparsely beset with simple hairs; sori medial to inframedial, with a small but persistent brown marginally setose indusium.

Thelypteris skinneri (Hook.) Reed, *Phytologia* 17: 314. 1968. *Aspidium skinneri* Hook. *Icon. Pl.* 10: t. 924. 1854, type from Guatemala [without further locality], *Skinner s.n.* (K). *Dryopteris skinneri* (Hook.) O. Ktze. *Rev. Gen. Pl.* 2: 813. 1891.

Uncommon, habitat unknown but probably wet low elevation forests, possibly along stream banks; Retalhuleu (see Maxon, *Proc. Biol. Soc. Wash.* 43: 87. 1930). British Honduras.

Rhizomes short-creeping, bearing several fasciculate fronds near the apex; stipes 5-8 cm. long, pubescent, scaly at the base; laminae 15-20 cm. long, 2-3 cm. broad, lanceolate, with ca. 2 pairs of oblong subentire free pinnae below, the lamina then becoming pinnatifid about $\frac{2}{3}$ to the midrib, ultimately shallowly lobed to the acuminate apex; veins 8-10 pairs per lobe, lowermost pairs from adjacent segments barely united below the

sinus or meeting the margin at the sinus; midrib and veins stellate-puberulent below, also with some longer stiff acicular hairs; leaf tissue chartaceous; sori medial to inframedial, indusiate, margin of indusia ciliate.

Thelypteris stolzeana A. R. Smith, *Phytologia* 34: 231. 1976.

Wet forests, about 1,360 m.; Alta Verapaz (type from along Río Carchá, between Cobán and San Pedro Carchá, Standley 90107, F). The only other known collection is from Chiapas.

Rhizomes erect, caudex ca. 1.0-1.5 cm. in diameter; stipes brownish, 10-20 cm. long, 1-2 mm. in diameter, with 2- to 3-cleft and a few simple hairs ca. 0.1 (0.2) mm. long, glabrescent; laminae dark gray-green, 15-25 cm. long, gradually reduced distally to a confluent, pinnatifid, somewhat elongate apex; rachises without buds; pinnae 8-9 pairs, sessile; largest pinnae to ca. 5 cm. long, 1.5 cm. broad, incised ca. 0.5-0.7; lowermost 1-2 pairs of pinnae slightly reduced and deflexed, narrowed at their base; segments suboblique, not or only obscurely falcate, 2-3 mm. broad, rounded to truncate at tip; veins 4-6 pairs per segment, the basal pair from adjacent segments meeting the margin at the sinus or the acroscopic vein of this pair meeting the margin within 0.3 mm. of the sinus; rachises and costae below with mostly 2- to 4-cleft (some simple), stalked hairs; leaf tissue chartaceous, on both sides glabrous, not verruculose; sori inframedial to medial, lacking indusia; sporangia glabrous.

Thelypteris tetragona (Swartz) Small, *Ferns SE States* 256. 1938. *Polypodium tetragonum* Swartz, *Prodr.* 132. 1788. *Polypodium subtetragonum* Link, *Hort. Berol.* 2: 105. 1833. *Dryopteris tetragona* (Swartz) O. Ktze. *Rev. Gen. Pl.* 2: 813. 1891. *D. subtetragona* (Link) Maxon, *Sci. Surv. Porto Rico* 6: 473. 1926. *T. subtetragona* (Link) E. St. John, *Amer. Fern J.* 26: 44. 1936.

Wet forests, limestone grottoes, stream banks, near sea level to 900 m.; Escuintla; Izabal; Petén; Retalhuleu; Santa Rosa. Florida, southern and eastern Mexico, British Honduras; Honduras, Panama; Antilles; Colombia to Suriname and Ecuador.

Rhizomes short-creeping, caudex ca. 1 cm. in diameter; fronds subdimorphic, the fertile ones erect, up to 1 m. long, long-stipitate, the sterile ones shorter, arching; stipes stramineous to tan, up to 60 cm. long, 2-5 mm. in diameter, stellate-pubescent; rachises without buds; laminae pinnate-pinnatifid with a conform terminal pinna, 30-45 (55) cm. long, 12-25 (30) cm. broad; pinnae 6-10 (12) pairs, subopposite, sessile to stalked 1 mm., lowermost somewhat narrowed at the base, 7-15 (18) cm. long; sterile pinnae mostly 2-3 cm. broad, fertile ones 1-2 cm. broad, pinnatifid 0.5-0.7 their width; segments oblique, subfalcate, rounded at the apex, ca. 4 mm. broad; veins 6-10 pairs, the basal pair united at an obtuse angle with an excurrent vein to the sinus; costae on both sides with mainly acicular hairs 0.1-0.3 mm. long; leaf tissue herbaceous, glabrous, not verruculose; sori inframedial, exindusiate; sporangia with simple setae 0.1 mm. long; $n = 72$.

Specimens of *T. tetragona* from western Guatemala are difficult to distinguish from *T. imbricata*, which see for additional discussion. Two specimens from this area (Maxon & Hay 3629, US, vicinity of Mazatenango; Rojas 536a, US, Quezaltenango, El Palmar) show abortive

spores. The Rojas specimen also shows giant globose (unreduced?) spores of the type discussed by Morzenti (Amer. Fern J. 52: 69-78. 1962).

Thelypteris toganetra A. R. Smith, Amer. Fern J. 63: 118. 1973.

Forming large often sterile colonies in wet forests and along rivers, shaded bluffs, 50-300 m.; Alta Verapaz; Petén. Mexico (San Luis Potosí to Oaxaca and Chiapas); British Honduras. Type from Veracruz, Atoyac River, *Copeland Herb.* 34 (UC).

Rhizomes long-creeping to suberect; fronds up to 70 cm. long, 30 cm. broad, with a conform terminal pinna; stipes and rachises on both sides glabrous, or above with a few stellate hairs less than 0.1 mm. long; pinnae 10-16 pairs, incised 0.5-0.7 their width, sessile, lowermost pinnae narrowed but still lobed at the base; segments subfalcate, acute at the apex; costae on both sides glabrous or above with a few simple hairs ca. 0.2 mm. long; costulae, veins, and leaf tissue on both sides glabrous, but frequently with scattered sessile reddish glands along the costules and veins below; veins 8-15 pairs, 1-2 lowermost pairs connivent at the sinus, not truly united; sori medial, exindusiate; sporangia glabrous; $n = 36$.

THELYPTERIS subg. **MACROTHELYPTERIS** (H. Ito) A. R. Smith, *Phytologia* 34: 233. 1976. *Thelypteris* sect. *Macrothelypteris* H. Ito in Nakai & Honda, Nov. Fl. Japan no. 4. 141. 1939. *Macrothelypteris* (H. Ito) Ching, *Acta Phytotax. Sin.* 8: 308. 1963.

Caudex short, creeping or suberect; fronds 2-pinnate to 2-pinnate-pinnatifid with \pm adnate pinnules; scales on rachis often with thickened bases, sometimes with marginal hairs, always with an acicular hair-tip; veins usually branched, not reaching margin; hairs on fronds acicular and capitate, some long-septate hairs always present; sori small, usually with a small indusium; sporangia usually with small capitate hairs near annulus; spores with a \pm winged perispore; $x = 31$.

Nine species, Old World tropics and subtropics, from Mascarene Islands to Queensland and Hawaii; a single species naturalized in various parts of the New World tropics and subtropics.

Thelypteris torresiana (Gaud.) Alston, *Lilloa* 30: 111. 1960. *Polystichum torresianum* Gaud. in Freyc. Voy. Bot. 333. 1828. *Aspidium uliginosum* Kunze, *Linnaea* 20: 6. 1847. *Dryopteris uliginosa* (Kunze) C. Chr. Index Fil. Suppl. 3. 100. 1934. *T. uliginosa* (Kunze) Ching, Bull. Fan Mem. Inst. Biol. Bot. 6: 342. 1936. *Macrothelypteris torresiana* (Gaud.) Ching, *Acta Phytotax. Sin.* 8: 310. 1963.

Adventive in the neotropics, along roadsides; Baja Verapaz. South-eastern United States; southern Mexico; El Salvador; Honduras; Costa Rica; Jamaica; South America; native to the warmer parts of Asia and the Pacific Basin.

Caudex short-creeping; stipes to 50 cm. long, glaucous when living, stramineous when dry, at the base with many narrow dark-brown hairy scales, the rest of the stipe glabrous or glabrescent; laminae to ca. 70 cm. long, 50 cm. broad, deeply 2-pinnate-pinnatifid, with 12-15 pairs of free pinnae, subbasal ones the longest; largest pinnae to ca. 20×9 cm., deltoid, pinnate with all pinnules but the lowest \pm adnate to a narrowly green-winged costa; pinnules distinctly oblique to the costae, lowest ones of basal pinnae reduced but of upper pinnae not so, largest $5-8 \times 1.5-2.5$ cm., cut almost to the costule into oblique dentate to deeply lobed segments 2.5-4 mm. wide; costae and costules beneath clothed with scattered pale, stiff, slender hairs, some multicellular and over 1 mm. long; leaf tissue below with short, erect, unicellular capitate hairs; veins in largest segments 7-12 pairs, forked or pinnate, distal part of each vein thickened; sori round, indusia very small with a few capitate hairs; sporangia each with 2-3 short capitate hairs near annulus; $n = 62, 93$.

THELYPTERIS subg. **MENISCIUM** (Schreber) Reed, *Phytologia* 17: 254. 1968. *Meniscium* Schreber, in Linn. Gen. Pl. ed. 8. 2: 757. 1791. *Dryopteris* subg. *Meniscium* (Schreber) C. Chr. Index Fil. XXII. 1906. *Thelypteris* subg. *Cyclosorus* sect. *Meniscium* (Schreber) Morton, Amer. Fern J. 53: 154. 1963.

Rhizomes creeping, stout, often 1-2 (2.5) cm. thick; fronds of most species large, up to 2 m. long, often subdimorphic; laminae 1-pinnate (simple in 2 spp.) with a terminal, often conform pinna; pinnae entire, or the margin repand, serrate, or uncinat-serrate; venation meniscioid (lateral veins straight and giving rise to numerous straight, arcuate, or subsigmoid secondary veins that regularly anastomose and produce an excurrent veinlet, thus creating a series of areoles between costa and pinna margin; hairs simple (never stellate), relatively sparse and short, curved, often confined to costae on both sides and main lateral veins below; sori confluent along the secondary veins and where they join, exindusiate; sporangia glabrous or with setae arising from the stalks; $x = 36$.

About 23 species, confined to the American tropics and subtropics, from southern Mexico to northern Argentina and Paraguay, Florida, Antilles. Most species occur at elevations below 1,500 m., along streams and wet banks.

- a. Pinnae uncinat-serrate, at least toward apex; sporangial stalks glabrous.
T. serrata.
- a. Pinnae entire, occasionally undulate or crenulate; sporangial stalks glabrous or with setae.
 - b. Sporangial stalks bearing near apex 1 or more stiff setae (seen as hairs among sporangia). *T. standleyi*.
 - b. Sporangial stalks without hairs.
 - c. Areoles of sterile pinnae almost as long as broad, the secondary veins nearly straight; pinnae up to 40 cm. long, mostly 2-3.5 cm. broad. *T. falcata*.
 - c. Areoles of sterile pinnae much shorter than broad, the secondary veins curving and arcuate, subsigmoid; pinnae less than 16 cm. long, 0.5-2.0 (2.3) cm. broad.
T. angustifolia.

Thelypteris angustifolia (Willd.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 57. 1953. *Meniscium angustifolium* Willd. Sp. Pl. 5: 133. 1810. *Dryopteris angustifolia* (Willd.) Urban, Symb. Antill. 4: 21. 1903.

Uncommon, wet thickets, ca. 300 m.; Retalhuleu; Suchitepéquez. Mexico (Puebla); Costa Rica; Panama; Colombia to Bolivia, Paraguay, Brazil; Greater Antilles.

Fronds 20-80 (130) cm. long, with stipes mostly 0.4-1.0 times as long as blades, fertile fronds longer-stipitate than sterile; laminae 1-pinnate, with 8-20 (22) pairs of lateral pinnae and a nearly conform terminal pinna; pinnae 5-16 cm. long, 0.5-2.0 (2.3) cm. broad, long-attenuate, entire, subequally cuneate at the base, stalked 2-10 mm.; lateral veins of sterile pinnae 11-18 pairs per 3 cm.; areoles 4- to 8-seriate, broader than long, the secondary veins arcuate or nearly straight; costae sparsely hairy above and below, veins and leaf tissue glabrous or nearly so on both sides; sporangial stalks without setae.

Thelypteris falcata (Liebm.) Tryon, Rhodora 69: 6. 1967. *Meniscium falcatum* Liebm. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. V. 1: 183. 1849. *Meniscium jurgensenii* Fée, Gen. Fil. 223. 1852. *Dryopteris falcata* (Liebm.) C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Afd. VII. 10: 270. 1913 (not Kuntze, 1891). *D. jurgensenii* (Fée) Maxon & Morton, Bull. Torrey Bot. Club 65: 360. 1938.

Locally common along shaded banks and streams, near sea level to 700 m.; Alta Verapaz; El Quiché; Izabal. Southern Mexico (type from Oaxaca, Distr. Chinantla, *Liebmman*, C!); British Honduras; Honduras to Panama; Colombia to Bolivia; Cuba.

Rhizomes short-creeping; fronds mostly 85-125 cm. long, 1-pinnate with a more or less conform terminal pinna; pinnae 8-12 pairs, subequal in length, the lower long-stalked (to 10-15 mm.), often curved, 15-32 (40) cm. long, (1.8) 2-3 (3.5) cm. broad, widest in the middle, tapering on both sides to an acuminate apex and a cuneate base, margin entire to undulate; veins meniscioid, with 6-9 series of areoles that are about as long as broad between costae and pinna margin, the secondary veins more or less straight and uniting at an obtuse angle, an excurrent vein often dividing the areole into 2 subequal trapeziform halves; costae above and below sparsely hairy (hairs 0.2-0.3 mm. long), the veins and leaf tissue on both sides glabrous or glabrescent; sori in a single row between costules, at the confluence of the secondary veins; sporangial stalk without hairs.

Thelypteris serrata (Cav.) Alston, Kew Bull. 1932: 309. 1932. *Meniscium serratum* Cav. Descr. Pl. 548. 1802. *Dryopteris serrata* (Cav.) C. Chr. Index Fil. 291. 1905.

Common in swamps, along river banks, wet thickets, 0-600 m.; Escuintla; Izabal; Retalhuleu; Santa Rosa. Florida; southern Mexico; Honduras to Panama; Antilles; South America to northern Argentina.

Rhizomes short-creeping; fronds up to ca. 2 m. long or more; laminae 1-pinnate, upper pinnae gradually shortened, with a lanceolate terminal segment; pinnae 15-25 pairs, the lower short-stalked to 4 mm., largest 15-25 cm. long, (2) 2.5-3.5 (4.5) cm. broad, the



FIG. 77. *Thelypteris* subgenus *Meniscium*. *T. falcata*. a, habit, $\times \frac{1}{2}$; b, portion of pinna, showing venation, $\times 1\frac{1}{2}$; c, sori, $\times 6$; d, bases of lower pinnae, $\times \frac{1}{2}$.

margin serrate or uncinat-serrate; fertile pinnae often somewhat narrower than the sterile ones; veins meniscioid, the secondary veins arcuate or subsigmoid, with 10-15 pairs anastomosing and giving rise to short excurrent veinlets, the areoles thus formed much shorter than broad; costae, costules, and sometimes veins and leaf tissue below pubescent (hairs ca. 0.2 mm.), above glabrous except for the sparsely hairy costae; buds occasionally borne at the base of costae of lower pinnae; sori along the veins at the anastomoses, confluent, exindusiate; sporangial stalks without hairs; $n = 36$.

Thelypteris standleyi (Maxon & Morton) Tryon, *Rhodora* 69: 8. 1967. *Dryopteris standleyi* Maxon & Morton, Bull. Torrey Bot. Club 65: 368. 1938.

Uncommon, brushy banks, 200-1,200 m.; Chiquimula, Izabal (type near Quiraguá, *Standley 24126*, US). Mexico (Chiapas); Honduras; Panama; Colombia to Bolivia.

Rhizomes short-creeping; fronds up to 1.9 m. long, with stipes much longer than lamina; laminae 1-pinnate, gradually reduced distally, up to 70 cm. long, 40 cm. broad; pinnae 12-17 lateral pairs with a terminal pinna, margin entire or slightly repand, (10) 12-22 cm. long and 2.3-4 cm. broad (the fertile often narrower), acute at the apex, rounded or subcordate at the base, all sessile; venation meniscioid, with 9-13 lateral veins per 3 cm. (13-15 on fertile fronds), the secondary veins arcuate or subsigmoid, acutely anastomosing to form 9-14 (20) series of areoles, excurrent venules free (secondary veins straight and obtusely united in fertile fronds); costae, veins, and sometimes leaf tissue below with curved, rigid hairs 0.2-0.3 mm. long, glabrous above except for scattered hairs along costae; sori oblong and confluent where the secondary veins anastomose; sporangia bearing rigid solitary setae from the sporangial stalk.

THELYPTERIS subg. **STEGNOGRAMMA** (Blume) Reed, *Phytologia* 17: 254. 1968. *Stegnogramma* Blume, Enum. Pl. Jav. 172. 1828. *Leptogramma* J. Smith, J. Bot. (Hooker) 4: 51. 1841. *Dryopteris* subg. *Leptogramma* (J. Smith) C. Chr., Ind. Fil. XXI. 1906.

Rhizomes short-creeping to erect; fronds pinnate, the pinnae entire to deeply pinatifid, the basal pinnae not or little reduced; upper pinnae broadly adnate to, and often decurrent on, the rachis and merging with the apical portion of lamina; rachises, costae, veins, and leaf tissue with acicular (unicellular or septate) hairs; glands lacking; veins free, meeting the margin at the sinus (ours), or anastomosing to form a complex network; aerophores absent; sori exindusiate, running along the veins; sporangia usually setiferous; spores finely spinulose; $x = 36$.

About 15 species, all but three confined to the Old World (mostly eastern Asia). *Thelypteris pilosa* is the sole species in North America; two species occur in southern Brazil.

Thelypteris pilosa (Mart. & Gal.) Crawford, Amer. Fern J. 41: 16, t. 3. 1951. *Gymnogramma pilosa* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 27, t. 4, f. 1. 1842. *Dryopteris pilosa* (Mart. & Gal.) C. Chr. Index Fil. 284. 1905. *Stegnogramma pilosa* (Mart. & Gal.) Iwatsuki, Amer. Fern J. 54: 141. 1964.

Wet shaded banks, slopes of ravines, rocky cliffs, 2,000-2,400 m.; Chimaltenango; Guatemala; Quezaltenango; San Marcos; Sololá. United States (Alabama); widely distributed in southern and western Mexico; Honduras. Syntypes from Veracruz, pic d'Orizaba, *Galeotti* 6267, 6268 (BR!).

Rhizomes short-creeping, ca. 2-5 mm. in diameter; fronds mostly less than 55 cm. long, with stipes 0.5-1.0 times the blade length; laminae shallowly to deeply pinnate-pinnatifid, up to 30 cm. long; pinnae 1-8 (10) cm. long, up to 1.4 (2.5) cm. broad, often broadly adnate and basiscopically decurrent to the rachis (especially in upper half of lamina), or the lowermost pinnae short-stalked (ca. 1 mm.), incised $\frac{1}{4}$ - $\frac{3}{4}$ their width; segments oblique, oblong to deltoid, mostly obtuse at the tip; veins 3-6 (10)-jugate, the 2 basal ones from adjacent segments running to the sinus; costae, costules, veins, and sometimes leaf tissue on both sides with long stout hairs mostly 0.5-1.5 mm. long; sori elongate along veins, mostly 1.5-4.0 mm. long, exindusiate; sporangia often minutely setose on the capsule, the setae ca. 0.1 mm. long; $n = 36$.

This species varies greatly in size of fronds, depth of cutting of pinnae, degree of adnation and decurrence of the pinnae, density and length of pubescence, and presence or apparent absence of sporangial setae. Crawford (Amer. Fern J. 41: 15-20. 1951.) recognized three varieties, including var. *major* (Fourn.) Crawford from Mexico and Guatemala. However, this variety seemingly intergrades with var. *pilosa*, and the two occur sympatrically. Thus I find no justification for recognition of varieties. Guatemalan specimens are mostly without sporangial setae, or have only obscure or occasional setae; most specimens throughout Mexico have decidedly setose sporangia. In *Thelypteris*, the presence or absence of sporangial setae is usually constant within a species; however, it is of doubtful taxonomic value here.

THELYPTERIS subg. **STEIROPTERIS** (C. Chr.) Iwatsuki, Mem. Coll. Sci. Kyoto Imp. Univ., ser. B, Biol. 31:31. 1964. *Dryopteris* subg. *Steiropteris* C. Chr. Biol. Arb. til. Eug. Warming 80. 1911. *Glaphyopteris* Presl ex Fée, Crypt. Vasc. Brésil 2:40. 1873. *Thelypteris* subg. *Glaphyopteris* (Presl ex Fée) Alston, J. Wash. Acad. Sci. 48:234. 1958.

Rhizomes creeping to suberect; blades with lowermost pinnae the longest or nearly so (1 species with auriculiform basal pinnae), pinnatifid to 1-pinnate-pinnatifid in most species; aerophores usually present at the base of costae, sometimes also at base of costules, the aerophores scalelike or peglike; veins running to the sinus or more or less connivent with a cartilaginous keel running from the sinus toward the costa (false vein), or veins meeting the margin just above the sinus and without false veins; costae and veins below with acicular hairs, these simple or septate, never stellate or hooked; glands absent on leaf tissue (present in 1 species); sori round to slightly oblong, indusiate or exindusiate (ours) in a few species; sporangia glabrous (setose in 2 species); spores with a winged sporoderm, the ridges narrow and sometimes anastomosing; $x = 36$.

About 20 species, confined to the American tropics. The bulk of species occurs in the Antilles and northern South America. I circumscribe the subgenus to include part of *Glaphyopteris* (*T. decussata* and allies), while referring the rest of *Glaphyopteris sensu* Christensen (*T. thomsonii* and allies) to subg. *Amauropelta*.

- a. Aerophores present at base of costules; reddish glands on leaf tissue below.
T. decussata.
- a. Aerophores absent at base of costules; reddish glands absent.
T. glandulosa var. *brachyodus*.

Thelypteris decussata (L.) Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 59. 1953. *Polypodium decussatum* L. Sp. Pl. 2: 1093. 1753. *Dryopteris decussata* (L.) Urban, Symb. Antill. 4: 19. 1903.

Uncommon, margins of wet forests, 300-700 m.; Alta Verapaz; Izabal. Nicaragua; Costa Rica; Panama; Antilles; Colombia to Peru and French Guiana; southern Brazil.

Rhizomes stout; fronds very large, up to 3.5 m. long; young stipes and croziers often mucilaginous; stipes up to 1.2 m. long, purplish brown, scaly at the base; laminae 1.0-2.3 m. long; pinnae 20-30 (45) cm. long, 2-3 (4) cm. broad, deeply incised to within 1 mm. of costae, lowermost the largest, with aerophores up to 10 mm. long at base of costae; segments perpendicular or slightly oblique, 3-4 mm. broad (4-5 mm. between costules), rounded or truncate at the tip, with scalelike aerophores 2-3 mm. long at base of costules; veins 20-40 (50)-jugate, close (ca. 18 per 1 cm.), prominulous above, lowermost pair reaching the margin above the sinus; leaf tissue glabrous above, beset with red sessile, hemispherical glands and a few erect hairs (0.1-0.2 mm.) below; costules and veins above with scattered stiff hairs (0.5-1.2 mm.), below with shorter, more numerous hairs ca. 0.1 mm. long, with a few longer hairs intermixed; sori medial to inframedial near the tips of segments, exindusiate; receptacle red-glandular; sporangia glabrous; $n = 36, 72$.

Thelypteris glandulosa (Desv.) Proctor var. **brachyodus** (Kunze) A. R. Smith, Phytologia 34:233. 1976. *Polypodium brachyodus* Kunze, Linnaea 9: 48. 1834. *Dryopteris brachyodus* (Kunze) O. Ktze. Rev. Gen. Pl. 2: 812. 1891. *T. brachyodus* (Kunze) Ching, Bull. Fan Mem. Inst. Biol. Bot. 6: 286. 1936.

Uncommon, in low-elevation forests, 50-350 m.; Alta Verapaz; Izabal. Mexico (Chiapas); British Honduras; Honduras to Panama and Peru.

Rhizomes stout, short-creeping to suberect, caudex 2-3 cm. thick; stipes often 50-80 cm. long, tan to brownish, glabrous; laminae 30-75 cm. long, abruptly narrowed above with a hastate terminal segment; pinnae alternate, 8-10 pairs, remote (5-8 cm.) up to 27 cm. long, the largest (lowest) mostly 3-4 cm. broad, lower distinctly stalked (to 5 mm.), with an aerophore to 2 mm. long at the base; pinnae narrowed at the base, incised scarcely to the middle; segments to 8 mm. broad (7-10 mm. between costules), subfalcate, rounded at the tip; veins 12-18 pairs per segment, the lower 3-4 forming narrow areoles between the costule and the sinus membrane; leaf tissue dark green above,

lighter green below, glabrous on both sides, the costae (sometimes costules and sinus membrane) beneath puberulous (hairs 0.1 mm. long); costae beneath with a few linear tan scales near the base; sori medial to inframedial toward segment apex, exindusiate; sporangia glabrous.

The type variety is confined to the Lesser Antilles and northern South America and differs slightly by its lighter green blades above, more falcate segments, and generally opposite pinnae. These differences are insufficient for recognition of *T. brachyodus* as a distinct species.

VITTARIA J. E. Smith

REFERENCES: R. C. Benedict, A revision of the genus *Vittaria* J. E. Smith, Bull. Torrey Bot. Club 41: 391-410. 1914. R. M. Tryon, Taxonomic notes IV: Some American vittarioid ferns, Rhodora 66: 110-117. 1964; and *Vittaria*, in: The ferns of Peru, Polypodiaceae, Contr. Gray Herb. 194: 211-219. 1964.

Plants small to medium-sized, epiphytic; rhizome small, short-creeping to erect, clathrate-scaly, the roots commonly densely golden-tomentose; leaves monomorphic, erect, or, more commonly, pendent, densely crowded to caespitose, simple, linear to linear-elliptic, entire, sessile to short-petiolate; petiole (when present) terete to flattened, often concolorous with, and scarcely distinguishable from, the lamina, not articulate to the rhizome; lamina glabrous, firm-herbaceous to subcoriaceous, margins plane to rather strongly revolute, the costa distinct to obscure, running the length of the lamina; veins anastomosing, forming a single series of narrow areoles on each side of the costa, lacking included veinlets; sporangia long-stalked, borne in deep to shallow grooves, in a single, continuous line on each side of the costa (sometimes nearly marginal); indusium lacking; paraphyses present and commonly abundant; spores monolete and bilateral, or trilete and tetrahedral, lacking perine, often mucilaginous.

Vittaria is a tropical or subtropical genus of some 60-70 species, with the larger majority occurring in the Old World. This genus of epiphytic, "shoestring" ferns is rather distinctive, with its linear, entire leaves, the two parallel, longitudinal lines of immersed sporangia, and the clathrate, often iridescent rhizome scales. However, within the genus many species are quite difficult to delineate, and actually the total may be much smaller than currently recognized.

- a. Petiole terete (at least at base) castaneous to atropurpureous, darker than the lamina; rhizome scales hairlike throughout, 2 cells broad, with a single longitudinal rib (or rarely 2-ribbed at base). *V. stipitata*.
- a. Petiole flattened, greenish or pale brown, concolorous with the lamina; rhizome scales 3-10 cells broad.
- b. Paraphyses orange to light brown, the apical cell not or scarcely dilated; spores monolete, bilateral; rhizome scales commonly tapering to a greatly elongated, filiform tip composed of a single longitudinal rib (this often $\frac{1}{3}$ - $\frac{1}{2}$ as long as the entire scale). *V. lineata*.

- b. Paraphyses deep reddish brown, the apical cell somewhat to greatly dilated; spores trilete, tetrahedral; rhizome scales attenuate, but the tip seldom tapering to a single longitudinal rib, or if so, the rib not greatly elongated. . *V. graminifolia*.

Vittaria graminifolia Kaulf. Enum. Fil. 192. 1824. *V. filifolia* Fée, Mém. Fam Foug. 3: 20. 1851-52.

Common fern of wet forests, pendent from limbs and trunks of trees, 900-3,200 m. (but found rarely at 100-200 m.); Alta Verapaz; Baja Verapaz; Chimaltenango; Chiquimula; Guatemala; Huehuetenango; Jalapa; Petén; El Progreso; Quezaltenango; El Quiché; San Marcos; Sololá; Totonicapán; Zacapa. West Indies; southern Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants epiphytic; rhizome dorsiventral, amply to densely scaly, the scales linear to lanceolate, grayish or light brown, highly iridescent, 3-6 mm. long, 0.3-0.8 mm. broad, commonly 4-10 cells (lumina) broad, attenuate, the tip not usually tapering to a single longitudinal rib, or if so, the rib not greatly elongated; leaves 8-45 cm. long, 0.08-0.25 cm. broad, sessile; petiole lacking or very short, flattened, pale green to light brown, usually concolorous with the lamina, essentially glabrous; lamina linear, opaque, plane to somewhat revolute, the midrib obscure or barely evident, broadly and shallowly sulcate adaxially; soral lines in deep grooves parallel with and 0.1-0.5 mm. from the margin; paraphyses deep reddish brown, the apical cell commonly conspicuously dilated; spores trilete, tetrahedral, or globose-tetrahedral.

This and *V. lineata* are often confused. Further comparison can be found under discussion of the latter.

Vittaria lineata (L.) J. E. Smith, Mem. Acad. Roy. Sci. (Turin) 5: 421. 1793. *Pteris lineata* L. Sp. Pl. 2: 1073. 1753.

Uncommon fern of wet lowland forests, pendent from limbs and trunks of trees, sea level to 80 m.; Izabal; Petén. Southern Florida; Georgia; West Indies; Mexico to Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants epiphytic; rhizome dorsiventral, amply to densely scaly, the scales linear, reddish to grayish brown, 4-8 mm. long, 0.1-0.3 mm. broad (or to 0.5 mm. at the dilated base), commonly 3-6 cells (lumina) broad, but tapering to a greatly elongated, filiform, tip composed of a single longitudinal rib, this tip often $\frac{1}{2}$ - $\frac{1}{2}$ as long as the entire scale; leaves 25-100 cm. long, 0.1-0.25 (0.3) cm. broad, sessile; petiole lacking or very short, flattened, pale green to light brown, usually concolorous with the lamina, essentially glabrous; lamina linear, opaque, plane to somewhat revolute, the midrib obscure or barely evident, broadly and shallowly sulcate adaxially; soral lines in deep grooves parallel with and 0.4-0.6 mm. from the margin (on very narrow laminae often midway between midrib and margin); paraphyses orange to light brown, the apical cell not or scarcely dilated; spores monolet, bilateral, fabiform.

The species is very rare in Guatemala, and is probably far less common throughout its range than currently recognized. Numerous specimens so determined in herbaria have proven to be, upon closer



FIG. 78. *Vittaria*. a-c, *V. graminifolia*: a, habit, $\times \frac{1}{2}$; b, portion of leaf, with some sporangia removed to show deep groove, $\times 12$; c, rhizome scale, $\times 12$; d, *V. lineata*, rhizome scale, $\times 12$; e, *V. stipitata*, rhizome scale, $\times 25$.

examination, *V. graminifolia*. The two species scarcely differ, other than in the features used in the key, and these characteristics are only discernible under high magnification. *Vittaria lineata* is a lowland fern, occurring at or near sea level. *Vittaria graminifolia* prefers higher altitudes, mostly between 1,000-3,000 m., although I have found two Guatemalan specimens, which were reported at 100-200 m.

Further comparison of these two species may be found below, under discussion of the excluded species, *V. dimorpha*.

***Vittaria stipitata* Kunze, Linnaea 9: 77. 1834.**

In wet forests, pendent on tree trunks, 50-350 m.; Alta Verapaz; Izabal; Petén. Greater Antilles; Nicaragua; Costa Rica; Panama; Colombia to the Guianas, south to Bolivia and Brazil.

Plants epiphytic; rhizome radial, amply provided with castaneous to blackish, filiform scales 2-3 mm. long, these 2 cells (lumina) broad, 1 row on either side of the single longitudinal rib, or 2-ribbed at the base; leaves 20-50 (70) cm. long, 0.3-0.6 (0.8) cm. broad, short-petiolate; petiole 1-5 (8) cm. long, terete (at least proximally), castaneous to atropurpureous, sparsely filiform-scaly at base; lamina linear, opaque, plane, the midrib obscure or barely evident; soral lines in deep grooves very near (0.1-0.4 mm.) the margin; paraphyses castaneous, very short, the apical cell abruptly and strongly dilated on the thin stalk; spores monolete, bilateral, narrow-fabiform.

EXCLUDED SPECIES

***Vittaria dimorpha* K. Müller, Bot. Zeit. 547. 1854.**

A number of specimens from Mexico and Central America are to be found in herbaria determined as *V. dimorpha*. This is supposedly a good species, nearly identical with *V. graminifolia* (spores tetrahedral; paraphyses dark reddish brown, with dilated apical cell) but having the filiform-tipped rhizome scales of *V. lineata*. I have not seen the type of *V. dimorpha*, but on all specimens so determined which I have examined there is indeed nothing to distinguish them from *V. graminifolia* except the shape of the rhizome scales, which seem to be intermediate between those of the latter and *V. lineata*. This character is, at best, a minor one, for the shape of the scales is rather variable. Commonly those of *V. lineata* are very long-attenuate, terminating in a tip composed of a single longitudinal rib. Such tips can equal the length of the rest of the scale, or they may be somewhat shorter; or, being very delicate, they may be broken off and missing completely. Scale tips of *V. graminifolia* commonly do not terminate in a single rib, or when they occasionally do, they are not as greatly elongated as in *V. lineata*. Apparently somewhere between these two conditions are supposed to lie the scales of *V. dimorpha*. *Vittaria graminifolia* and *V.*

lineata are so similar that if it were not for the difference in shape of spores, it is likely they would be considered only varietally distinct. Thus, to recognize yet another "species" intermediate between these two seems to stretch the species concept beyond a reasonable limit.

Among dozens of specimens I have examined, only one such intermediate has been found from Guatemala; *Maxon & Hay 3401*, from Salamá, Baja Verapaz, ca. 900 m. (US). I recognize this simply as a variant of *V. graminifolia*.

WOODSIA R. Brown

REFERENCE: Donald F. M. Brown, A monographic study of the fern genus *Woodsia*, Beih. Nova Hedwigia 16: 1-154. 1964.

Plants epipetric, or rarely in soil near rocks; rhizome stout, horizontal to obliquely ascending, thickly invested with brownish scales, these often with a darker brown or black central band; leaves numerous, caespitose, monomorphous, to 60 cm. long; petiole stramineous to dark brown, articulate and regularly deciduous, or (in ours) continuous and breaking away irregularly; pinnae few to many pairs, subdistant to crowded, simple to pinnate, firm-herbaceous to subcoriaceous; veins free, pinnately arranged; sori abaxial on the veins; indusia globose to irregularly saucer- or cup-shaped (as in ours), or merely subtended by trichomes or hairlike scales; sporangia stalked; spores bilateral, monoletе, variously sculptured, commonly 32-64 in each sporangium.

Woodsia is a cosmopolitan genus, consisting of 23 species which are distributed chiefly throughout boreal or temperate zones of Europe and Asia. A single species is found in South America. Three others are in Mexico, one of which is also found in Guatemala.

Woodsia mollis (Klf.) J. Sm. J. Bot. (London) 4: 191. 1841. *Physematium molle* Klf. Flora 1829: 341. 1829. *W. mexicana* R. Br. in Wall. Pl. Asiat. Rar. 1: 41. 1830 (not *W. mexicana* Fée, 1857). *W. guatemalensis* Hook. Sp. Fil. 1: 60, t. 21a. 1844 (type from Guatemala, location unspecified, *Skinner s.n.*). *Diacalpe guatemalensis* Trevis. Nuovo Giron. Bot. Ital. 7: 160. 1875.

On exposed or shaded banks or outcrops, or on talus slopes, 1,800-3,400 m.; Chimaltenango; Guatemala; Huehuetenango; Jutiapa; Quezaltenango; San Marcos; Sololá; Totonicapán. Mexico; El Salvador.

Rhizome stout, short, horizontal to obliquely ascending, rather abundantly provided with scales, these light or reddish brown, usually with a lustrous black center and ciliate (often obscurely so); leaves numerous, caespitose, 10-50 cm. long, 2-6 cm. broad; petiole terete or slightly flattened, not articulate, light brown to stramineous (or old remnants grayish), provided at and near the base with scales as on the rhizome, above the base sparsely scaly and pubescent; lamina chartaceous or subcoriaceous, narrow-elliptic, tapered gradually to apex and base, pinnate-pinnatifid to sub-bipinnate; rachis provided with a few brown scales, and pilose with light-brown, lax, septate trichomes; pinnae numerous, subdistant, sessile, broadly to narrowly deltoid, incised deeply or quite to the



FIG. 79. *Woodsia mollis*. a, habit, $\times \frac{1}{2}$; b, rhizome scales, $\times 15$; c, base of fertile pinna, $\times 5$; d, sorus, greatly enlarged.

costa; ultimate segments or pinnules obtuse, crenate to shallowly lobed, pubescent on both sides, the trichomes on the adaxial side whitish, appressed, those of the margin and abaxial side light brown, lax, spreading; veins free, pinnately arranged in each segment, prominent abaxially, somewhat immersed adaxially; sori usually 2-4 pairs per segment, supramedial between midrib and margin; indusium subglobose, usually opening and becoming roughly cup-shaped at maturity, with the sides often lacerate, commonly containing 5-10 sporangia.

This can be confused with no other species of *Woodsia* in the New World. Of the American species with nonarticulated petioles, it is the only one with globose indusia.

WOODWARDIA J. Smith

Plants large, coarse, terrestrial; rhizome stout, abundantly scaly, erect to (less commonly) creeping; petiole stout, not articulate, glabrous above, densely scaly at base; lamina commonly pinnate-pinnatifid, gradually tapering to a pinnatifid apex, chartaceous to subcoriaceous, glabrous or somewhat scaly (especially abaxially); rachis glabrous or scaly, the scales sometimes intermixed with minute, filamentous squamulae, terete to subquadrangular, often canaliculate adaxially, in a few species bearing proliferous buds adaxially at the bases of pinnae; pinnae stalked or sessile, ascending, or basal ones spreading, strongly lobed, or incised deeply (often almost quite) to the costa, costae continuous onto the rachis; ultimate lobes or segments entire to serrate or spinulose-serrate; veins copiously anastomosing, especially along the costae and (sometimes) costules, then becoming free toward the margin; sori in a chainlike series, each borne on the distal vein of the costular areole, superficial, or deeply immersed (and then the adaxial side of the pinnae appearing embossed); indusium thick-textured, attached along the distal edge of the sorus, opening toward the costule, about the same shape, and nearly the same size, as the areole, persistent; paraphyses lacking; sporangia stalked, the stalks commonly long and slender; spores monolete, bilateral, with perine.

Woodwardia is a genus of 8-10 species, with a greatly disjunct distribution, occurring in predominantly temperate regions of both hemispheres. Most workers prefer to exclude the North American fern *W. areolata* (L.) Moore from the genus, principally on the character of the dimorphic leaves. This is more commonly treated as a monotypic genus, *Lorinseria* Presl.

In Central America, *Woodwardia* is represented by a single species.

***Woodwardia spinulosa* Mart. & Gal. Nouv. Mém. Acad. Roy. Sci. Bruxelles 15: 64. 1842.**

In wet forests, thickets, and shaded ravines, often on steep banks or near streams or waterfalls, 1,500-2,800 m.; Alta Verapaz; Chimaltenango; Chiquimula; Huehuetenango; Jalapa; Quezaltenango; El Quiché; Sacatepéquez; San Marcos; Santa Rosa; Sololá; Zacapa. Mexico; Honduras; El Salvador; Nicaragua; Costa Rica.

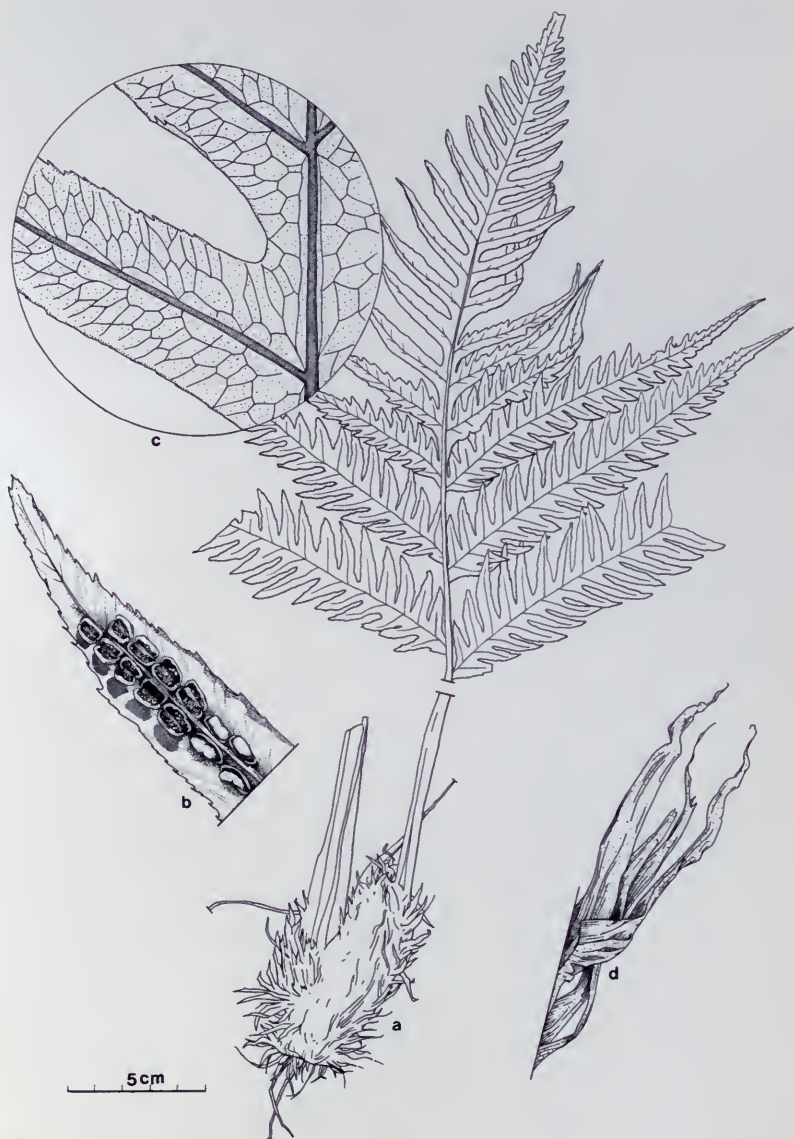


FIG. 80. *Woodwardia spinulosa*. a, habit, $\times \frac{1}{2}$; b, portion of fertile segment, $\times 3$; c, venation, $\times 3$; d, rhizome scales, $\times 5$.

Plants terrestrial; rhizome erect or ascending, copiously scaly, the scales about 1-2 cm. long, lanceolate or linear-lanceolate, entire, thin-textured, the apex often long-attenuate; leaves 0.5-1.7 m. long, 0.25-0.6 m. broad, caespitose; petiole 20-70 cm. long, shorter than the lamina, yellow-brown to stramineous, but commonly dark brown at the densely scaly base, glabrous or sparsely scaly distally, or sparsely and minutely scurfy; lamina ovate or subdeltoid, adaxially glabrous, abaxially provided with a scattering of minute, deep-orange scales; rachis yellow-brown or stramineous, sparsely scaly (and sometimes scurfy) as on the petiole; pinnae short-stalked or sessile, often adnate basiscopically, lanceolate, tapered to a narrowly acute or attenuate, spinulose apex, incised very deeply; ultimate segments numerous, narrow, acute to attenuate, subfalcate, the margins spinulose-serrate, joined with adjacent segments by a narrow, acute (V-shaped) or broad, obtuse (U-shaped) sinus; veins distinct (at least abaxially), copiously areolate, the costules connected by a single narrow, costular areole, and always 1 (and commonly 2) series of areoles present between costule and each margin, the ultimate veinlets free, terminating at the segment margin in usually conspicuous, enlarged hydathodes; sori conspicuous, deeply impressed in the tissue, often nearly filling the costular areole, 1-3 mm. long; indusium oblong, convexly curved over the sporangia, firm, persistent, drying gray-brown to (most commonly) reddish brown, subentire to undulate-crenulate.